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Illustrated identification keys to strongylid parasites (strongylidae: Nematoda) of horses, zebras and asses (Equidae)

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Abstract

The Equidae (the horse, *Equus caballus*, the ass, Equus asinus, zebras and their hybrids) are hosts to a great variety of nematode parasites, some of which can cause significant morbidity or mortality if individual hosts are untreated. Worldwide the nematode parasites of horses belong to 7 suborders, 12 families, 29 genera and 83 species. The great majority (19 of 29 genera and 64 of 83 species) are members of the family Strongylidae, which includes the most common and pathogenic nematode parasites of horses. Only the Strongylidae are included in this treatise.

The Strongylidae (common name strongylids) of horses – nematodes with a well-developed buccal capsule, a mouth collar with two leaf-crowns, and a strongyloid (common name of superfamily Strongyloidea) copulatory bursa – can be separated into two subfamilies: Strongylinae (common name strongylins), usually large or medium-sized with a globular or funnel-shaped buccal capsule; and Cyathostominae (common name cyathostomins), usually small to medium-sized with a cylindrical buccal capsule.

The increased attention to strongylid nematode parasites of horses has resulted in the need for updated diagnostic keys to these parasites using readily recognizable characters and the most recent literature on their systematics. Because the cyathostomins have been historically difficult to identify, and because they have emerged as the most significant nematode pathogens of horses, we provide a brief nomenclatural and taxonomic history and an introduction to the morphology of this group. This treatise is intended to serve as a basic working tool—providing easy identifications to genus and species of adult strongylid nematodes of equids. All strongylid nematodes normally parasitic in horses, the ass (and their hybrids), and zebras are included. The keys are illustrated with line drawings and halftone photomicrographs of each species. A short discussion of the systematics of the genus and species is provided for each genus following the species descriptions. Species diagnoses and a synonymy of each species is provided. Geographic distribution, prevalence, and location in host are also given for each species.

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Keywords: Cyathostominae; Strongylinae; Taxonomy; Classification; Equids; Parasites

1. Introduction

The horse, *Equus caballus*, the ass, *Equus asinus*, zebras and their hybrids are hosts to a great variety of nematode parasites, most of which have traveled the world with their hosts. The nematodes normally parasitic in equids fall into 7 suborders, 12 families, 29 genera, and 83 species. The great majority (64 of 83

Abbreviations: ELC, external leaf crown; ILC, internal leaf crown; MC, mouth collar; BC, buccal capsule; NR, nerve ring; S, support of ELC; SI, septum intracoronare; EI, esophageal–intestinal junction.

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species) are members of a single family, the Strongylidae. The 64 species, in 19 genera, of the family Strongylidae, are the most common and economically important nematode parasites of horses. The 19 non-strongylid nematode species, scattered in 10 different families, are for the most part well known and easily identifiable (Lichtenfels, 1975) and are not included here.

The Strongylidae (common name strongylids) of horses – nematodes with a well-developed buccal capsule, a mouth collar with two leaf-crowns, and a strongyloid (common name of Superfamily Strongyloidea) copulatory bursa – can be separated (Lichtenfels, 1980) into two subfamilies: Strongylinae (common name strongylins), usually large or medium-sized with a globular or funnel-shaped buccal capsule; and Cyathostominae (common name cyathostomins), usually small to medium-sized with a cylindrical buccal capsule. In this treatise 14 species of Strongylinae of domestic equids are organized in 5 genera: *Strongylus*, *Oesophagodontus*, *Triodontophorus*, *Bidentostomum* and *Craterostomum*. This five-genera system is accepted by most taxonomists except that Skrjabin and his students subdivided the genus *Strongylus* into three genera following Ershov (1943). The reasons we do not follow Ershov (1943) are given in the Discussion of the genus *Strongylus*. The 14 species of strongylins are relatively easy to identify, in comparison to the 50 closely related species of cyathostomins.

The 50 species of the Tribe Cyathostominea (all species of the subfamily Cyathostominae parasitic in equids) (Lichtenfels et al., 1998) are organized in 14 genera: *Cyathostomum* Molin, 1861 sensu stricto; *Coronocyclus* Hartwich, 1986, *Cylicocyclus* Ihle, 1922; *Cylicodontophorus* Ihle, 1922; *Tridentoinfundibulum* Tshoijo in Popova, 1958; *Cylicostephanus* Ihle, 1922; *Skrjabinodentus* Tshoijo in Popova, 1958; *Petrovinema* Ershov, 1943; *Parapoteriostomum* Hartwich, 1986; *Poteriostomum* Quiel, 1919; *Gyalocephalus* Looss, 1900; *Hsiungia* K'ung and Yang, 1964; *Caballonema* Abuladze, 1937; and *Cylindropharynx* Leiper, 1911. More detailed discussion of the bases for placing various species in particular genera can be found in the Discussion following each key to species.

Because the cyathostomins have been historically difficult to identify, and because they have emerged as the most significant nematode pathogens of horses (Herd, 1990), we provide below a brief nomenclatural and taxonomic history and an introduction to the morphology of this group.

The Cyathostominea are the most common nematode parasites of horses and can cause considerable morbidity and mortality (Herd, 1990). Research activity on these nematodes is high because: (1) larval cyathostominosis (previously cyathostomosis or cyathostomiasis), a syndrome in which large numbers of larvae emerge from the walls of the large intestine and caecum and cause severe colitis that may result in death, is recognized increasingly (Mair, 1994; van Loon et al., 1995); (2) resistance to anthelmintics within the Cyathostominea has been reported widely (Fisher et al., 1992) and (3) biological control prospects, using nematode-trapping fungi, appear to be promising (Larsen et al., 1996).

Infections with these nematodes typically consist of very large populations and numerous species. A total of 50 species of cyathostomins are recognized as valid species parasitic in horses, donkeys, and zebras worldwide (Lichtenfels et al., 1998; Matthee et al., 2002), but 10 of these species have been reported only from zebras or donkeys, and a few others have been reported only rarely (Lichtenfels et al., 1998). Surveys worldwide have reported about 16–24 species of the Tribe Cyathostominea in most regions and from 4 to 14 species with a prevalence of 50% or higher (Reinemeyer et al., 1984; Carvalho et al., 1998; Lyons et al., 1999; Lichtenfels et al., 2001). However, the prevalence of the less common species is greatly underestimated. Chapman et al. (2003) reported that 9–15 species were found in a single animal when 200 worms were identified, but the number increased to 20–29 when all nematodes in a 5% aliquot were identified. Thus, most individual horses carry a burden of 5–10 common species (and several to many less common species), including many thousands (sometimes more than 100,000) of lumen-dwelling adult nematodes. In addition, populations of developing larval stages in the walls of the large intestine may be as large or larger than populations of adults in the lumen (Reinemeyer et al., 1984; Bucknell et al., 1995).

The major challenges to understanding and controlling these parasites are the species complexity of the nematode populations, our inability to morphologically identify eggs in feces and the difficulty in identifying larvae on pasture. Adult nematodes can be identified to species by only a few authorities using comparative anatomy. Larval stages are exceptionally difficult to identify and eggs are impossible to identify to even the subfamily level. Research worldwide on the development of diagnostic DNA markers, on the testing of biological and biochemical control agents is hampered by the need to collect specimens from sacrificed horses. However, recent studies (Kaye et al., 1998; McDonnell et al., 2000; Hung et al., 2000; Hodgkinson et al., 2001, 2005; Lichtenfels et al., 2002) have examined

molecular relationships of these species with a view to: (1) preparing a predictive classification and (2) developing molecular markers for use in identification of both pre-parasitic and parasitic stages.

This increased attention to strongylid nematode parasites of horses has resulted in the need for updated diagnostic keys to these parasites using readily recognizable characters and the most recent literature on their systematics.

This treatise is intended to serve as a basic working tool—providing easy identifications to genus and species of adult strongylid nematodes of equids. All strongylid nematodes normally parasitic in horses, the ass (and their hybrids), and zebras are included.

This treatise consists of illustrated keys to genera and to species. The keys are illustrated with line drawings and halftone photomicrographs of each species. Illustrations are original unless noted otherwise.

A short discussion of the systematics of the genus and species is provided for each genus following the species descriptions. Species diagnoses and a synonymy of each species is provided. Geographic distribution, prevalence, and location in host are also given for each species.

2. History

The validity of the genus *Cyathostomum* and its type species *C. tetracanthum* has had a contentious history (Lichtenfels, 1975; Hartwich, 1986; Gibbons and Lichtenfels, 1999). The validity of *Cyathostomum* and its type species was finally established recently by the International Commission on Zoological Nomenclature (ICZN) (Opinion, 1972 on Case 3075, June 2001). A few highlights of the history of the controversy and its solution are summarized here. This history is primarily about the generic level classification of the Cyathostominea. The history of species level differences will be discussed following the keys to species of the various genera.

Molin (1861) established *Cyathostomum*, with *Strongylus tetracanthus* as the type species, by monotypy. Looss (1900) recognized that Molin's *C. tetracanthum* included several species and restricted the name to the most common species found by him in Egypt. Railliet (1923) proposed that *Cyathostomum* was a homonym of *Cyathostoma* Blanchard, 1849 and substituted *Trichonema* Cobbold, 1874. For many years both *Trichonema* and *Cyathostomum* were used for overlapping groups of species by various experts. Mclntosh established (International Commission ruling; Hemming, 1943) that *Cyathostomum* was not a homonym of *Cyathostoma* and listed a synonymy of the type species (McIntosh, 1951). Lichtenfels (1975) reviewed the history of the controversy and followed McIntosh's recognition of *Cyathostomum*, with *C. tetracanthum* as the type species. Hartwich (1986) discovered Molin's (1861) type series of *C. tetracanthum* and determined that the species designated by Looss (1900) as *C. tetracanthum* is not present among Molin's specimens. Hartwich selected and renamed *C. catinatum* Looss, 1900 as the true *C. tetracanthum* and renamed Looss' *C. tetracanthum* as *C. aegyptiacum*. In the interest of stability, the Sun City Workshop (Lichtenfels et al., 1998) voted (with the concurrence of Dr. Gerhard Hartwich) to ask the International Commission on Zoological Nomenclature to validate the names of these species in use prior to Hartwich's proposal (Gibbons and Lichtenfels, 1999). Only Dvojnos and Kharchenko (1994) had followed Hartwich and referred to *C. catinatum* as *C. tetracanthum*. The ICZN ruled (Opinion 1972, 2001): "Ruling

(1) Under the plenary power all previous fixations of type specimens for the nominal species *Strongy1us tetracanthus* Mehlis, 1831 are hereby set aside and the specimen no. 087757.00 in the U.S. National Parasite Collection, Beltsville, Maryland, collected by A. Looss in 1899, is designated as the neotype.
(2) The name *Cyathostomum* Molin, 1861 (gender: neuter), type species by monotypy *Strongy1us tetracanthus* Mehlis, 1831, is hereby placed on the Official List of Generic Names in Zoology.
(3) The following names are hereby placed on the Official List of Specific Names in Zoology:
    (a) *tetracanthus* Mehlis, 1831, as published in the binomen *Strongylus tetracanthus* and as defined by the neotype designated in (1) above (specific name of the type species of *Cyathostomum* Molin, 1861),
    (b) *catinatum* Looss, 1900, as published in the binomen *Cyathostomum catinatum*.
(4) The following names are hereby placed on the Official Index of Rejected and Invalid Generic Names in Zoology:
    (a) *Cylichnostomum* Looss, 1901 (a junior objective synonym of *Cyathostomum* Molin, 1861),
    (b) *Cylicostomias* Railliet, 1901 (a junior objective synonym of *Cyathostomum* Molin, 1861).
(5) The following names are hereby placed on the Official Index of Rejected and Invalid Specific Names in Zoology:
    (a) *hexacanthum* Wedl, 1856, as published in the binomen *Sclerostoma hexacanthum* (a junior objective synonym of *Strongy1us tetracanthus* Mehlis, 1831),

(b) *aegyptiacum* Railliet, 1923, as published in the binomen *Trichonema aegyptiacum* and as defined by the lectotype designated by Gibbons and Lichtenfels (1999) (a junior objective synonym of *Strongylus tetracanthus* Mehlis, 1831)."

Major contributions and schemes of classification for the Cyathostominea were made by Ihle (1922), Ershov (1943), McIntosh (1951), K'ung (1964), Lichtenfels (1975), Hartwich (1986), Dvojnos and Kharchenko (1994), Lichtenfels et al. (1998) and Zhang and K'ung (2002). In the following paragraphs the systems of these workers are described briefly.

The system of Ihle (1922) organized 20 species in 7 groups – 5 of which he designated as subgenera – all in the genus *Cylicostomum*, which is a synonym of *Cyathostomum*, Ihle's 5 subgenera were *Cylicostomum*, *Cylicocercus*, *Cylicocyclus*, *Cylicostephanus*, and *Cylicodontophorus*. His other groups were the *Brevicapsulatum*-group and the *Montgomeryi*-group. Cram (1924) raised all the subgenera of Ihle (1922) to generic rank, placed the *Brevicapsulatum*-group in the genus *Cylicobrachytus* Cram, 1924, and the *Montgomeryi*-group in *Cylicotoichus* Cram, 1924.

The system of McIntosh (1951) was essentially identical to that of Ihle (1922) as modified by Cram (1924) except that *Cylicotoichus* was omitted (probably because *C. montgomeryi* is a parasite of the zebra not known from domestic equines) and *Cylicotetrapedon* Ihle, 1925, was added.

The system of Ershov (1943) divided *Cyathostomum*, sensu lato into five genera including *Trichonema*, *Cylicocyclus*, *Cylicodontophorus*, *Petrovinema* Ershov, 1943, and *Schulzitrichonema* Ershov, 1943.

In 1964 K'ung reorganized Cyathostomum, sensu lato. He substituted *Trichonema* for *Cylicostephanus* and accepted *Cyathostomum*, *Cylicocyclus*, *Cylicodontophorus*, *Cylicotetrapedon*, *Petrovinema*, and *Skrjabinodentus* Tschoijo, 1957.

Lichtenfels (1975) modified the earlier schemes evolved by Ihle, Cram, and McIntosh as follows:

1. The genus *Cylicocercus*, which was distinguished primarily by the bent female tail, was eliminated by placing 3 species (*C. alveatum*, *C. catinatum*, and *C. pateratum*) in *Cyathostomum* and 1 species (*C. goldi*) in *Cylicostephanus*.
2. The species of *Cylicotetrapedon*, which were distinguished by the presence of teeth in the esophageal funnel, were included in *Cylicostephanus*, as suggested by Foster (1936).
3. The two species of *Cylicobrachytus* (*C. prionodes* and *C. brevicapsulatum*) were placed in *Cylicocyclus* following Ershov (1939) and K'ung (1964).
4. *Cylicodontophorus ultrajectinus* was moved to *Cylicocyclus* following Ershov (1939).

Lichtenfels (1975) modified the scheme of Ershov (1943) as follows:

1. The species of *Trichonema* were assigned to either *Cyathostomum* or *Cylicostephanus*.
2. Two species, *C. pateratum* and *C. sagittatum*, were moved from *Cylicodontophorus* to *Cyathostomum*.
3. The genus *Schulzitrichonema* Ershov, 1943, distinguished by teeth in the esophageal funnel and identical to *Cylicotetrapedon* Ihle, 1925, was eliminated and the species assigned to *Cylicocyclus* (*C. leptostomum*) or *Cylicostephanus* (*C. asymetricus* and *C. goldi*).
4. *Petrovinema* was eliminated by transferring the two species to *Cylicostephanus*.
5. *Cylicodontophorus ornatum* was moved to *Cylicostephanus*.

The system of Lichtenfels (1975) differed from the system of K'ung (1964) as follows:

1. *Trichonema*, was not accepted as a substitute for *Cylicostephanus*.
2. The species of the genus *Petrovinema* were included in *Cylicostephanus*.
3. The species of the genus *Cylicotetrapedon* were included in *Cylicostephanus*, except for *C. leptostomum*, which was placed in *Cylicocyclus*.

Hartwich (1986) restudied the Cyathostominea, providing useful new cephalic characters (see Section 3), a detailed history and a revision of the generic classification of the tribe. Except for his ill-fated proposal (see above) to change the names of *Cyathostomum catinatum* (to *C. tetracanthum*) and *C. tetracanthum* (to *C. aegyptiacum*), his classification of the tribe differed little from that of Lichtenfels (1975). Changes in the classification proposed by Hartwich (1986) included the establishment of two new genera: *Coronocyclus* to include four species – *C. coronatus*, *C. labiatus*, *C. labratus* and *C. agittatus* – that Lichtenfels (1975) had included in *Cyathostomum*; and, *Parapoteriostomum* to include three species – *P. mettami*, *P. euproctus* and *P. schuermanni* – that Lichtenfels (1975) had included in *Cylicodontophorus*. Hartwich (1986) also differed with Lichtenfels (1975) by recognizing

Petrovinema Ershov, 1943 as separate from *Cylicostephanus*. In addition, Hartwich (1986) did not include *Gyalocephalus* in the *Cyathostominea*.

The complete classification of the strongylids of horses provided by Dvojnos and Kharchenko (1994), unique in its descriptions of parasitic fourth-stage larvae of many species, included a generic classification of the Cyathostominae of horses that differed somewhat from that of Hartwich (1986). Dvojnos and Kharchenko (1994) recognized two genera proposed by Tshoijo, in Popova (1958)—*Tridentoinfundibulum* for the single species *T. gobi*, and *Skrjabinodentus* for *S. caragandicus* and *S. tshoijoi*, species not studied by Hartwich, and differed with him by not recognizing *Parapoteriostomum* and by recognizing *Cylicotetrapedon* Ihle, 1925 for two species—*C. asymetricus* and *C. bidentatus*. Unfortunately, Dvojnos and Kharchenko (1994) followed the ill-fated proposal of Hartwich (1986) (see above) to rename *C. catinatum* as *C. tetracanthum* and to rename *C. tetracanthum* as *C. aegyptiacum*. Thus, users of the 1994 paper by Dvojnos and Kharchenko must be careful to avoid the confusion of names for these species used therein. To our knowledge, Dvojnos and Kharchenko (1994) were the only authors to follow the ill-fated proposal of Hartwich (1986) to rename these species.

In part, to avoid the confusion expected by the proposed renaming of *C. tetracanthum* and *C. catinatum*, a series of international workshops were convened at meetings of the World Association for the Advancement of Veterinary Parasitology in 1997, 1999 and 2001 (Lichtenfels et al., 1998, 2002). The first of these workshops, at Sun City, Republic of South Africa, resulted in 2 major advances: (1) a checklist of 93 genus and species level names for 51 [now 50] recognized species of the Cyathostominea (Lichtenfels et al., 1998) and (2) an agreement, in the interest of stability, to ask the International Commission on Zoological Nomenclature (ICZN) to validate the names *Cyathostomum tetracanthum* and *Cyathostomum catinatum* of Looss (1900). This nomenclatural adjudication was required to resolve an ambiguity over which species should bear the names *C. tetracanthum* and *C. catinatum* following the discovery by Hartwich (1986) of long-lost types of the former species. The ICZN granted the request to preserve the common usage prior to Hartwich's (1986) discovery and to validate the names of Looss (1900) (Opinion 1972 on Case 3075 was published in Bulletin of Zoological Nomenclature, June 2001; details above). The Checklist of Recommended generic and specific names for the Cyathostominea was published (Lichtenfels et al., 1998) and differed only slightly from the names used in this treatise. The 1998 Checklist included the same 14 genera as in the present treatise, and differs from the generic system of Dvojnos and Kharchenko (1994) in not recognizing *Cylicotetrapedon*, and by recognizing *Parapoteriostomum*. The number of species recognized in the present treatise (50) differs from the 1998 checklist by the addition of *Cylicocyclus asini*, a new species described by Matthee et al. (2002), and *Cylicocyclus adersi* and *Cylicocyclus gyalocephaloides*, two recently redescribed species listed in the 1998 checklist as species inquirendae; and by the recognition herein of only three of the eight species of *Cylindropharynx* listed in the 1998 checklist.

In illustrated keys to nematode parasites of horses, Zhang and K'ung (2002) followed the generic classification of the Cyathostominea recommended by Lichtenfels et al. (1998).

3. Morphology

The members of the Tribe Cyathostominea are the most difficult strongylid nematodes of horses to identify to species level. However, with careful attention to the characteristics of the mouth collar, cephalic papillae, internal leaf-crown (ILC) and external leaf-crown (ELC), extra-chitinous supports (S) of the ELC, buccal capsule, and esophageal funnel these species of small to medium-sized strongylids are readily recognizable.

Characteristics of the posterior ends of males and females can also be useful, or essential, for identifying some species (Fig. 1).

Most of the cephalic characters listed above have been used by almost all previous workers, and can be identified readily with reference to Fig. 1. Other characters, including extra-chitinous supports, septum intracoronare, and inner and outer rings of the mouth collar can be difficult to identify for inexperienced workers, and will be described here with reference to appropriate figures.

Extra-chitinous supports of the ELC consist of a sclerotized ring anterior to the buccal capsule. It sometimes appears to be a continuation of the buccal capsule, as in the genus *Cyathostomum* (Figs. 27–36), but it is usually connected by strands of connective tissue to the buccal capsule, the mouth collar, and to the elements of the ELC (Figs. 36–126). Looss (1902) referred to this structure as "problematic structure in substance of mouth collar," and described and illustrated it in *C. tetracanthum*, *C. coronatum*, *C. catinatum*, *C. labratum*, and *C. labiatum*. This terminology was followed by Ihle (1922) and Skladnik (1935). Theiler (1924) changed the name of this structure to "extra-chitinous supports of the external

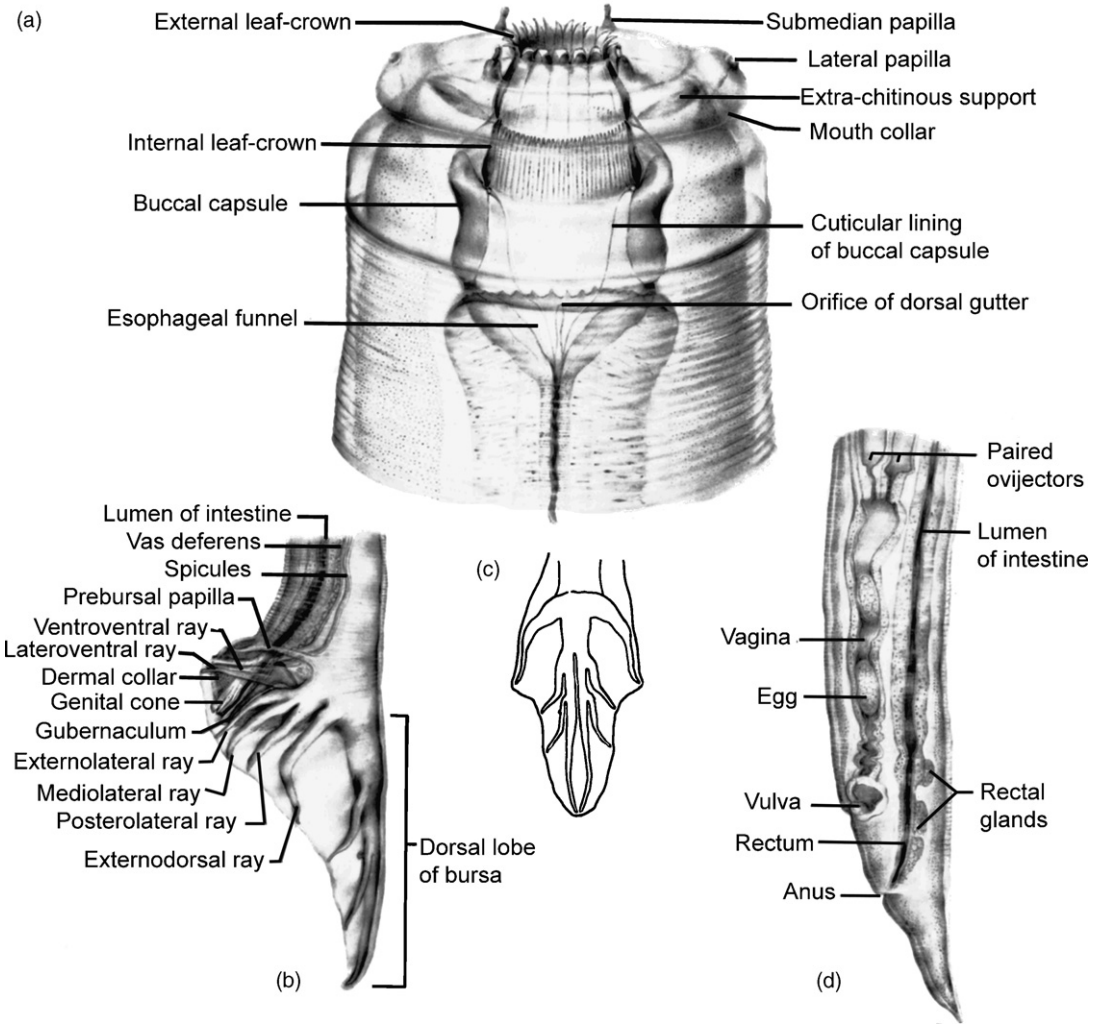

Fig. 1. *Coronocyclus coronatus*, labeled drawings, showing characteristics of Strongylidae. (a) Head, ventral view. (b) Male tail, lateral view. (c) Dorsal lobe of bursa of male tail, dorsal view. (d) Female, lateral view of posterior end. (Modified from Lichtenfels, 1975).

leaf-crown''. She described this structure in *C. sagittatum* in addition to those mentioned by Looss (1902) above. Lichtenfels (1975) and Hartwich (1986) have previously attached systematic importance to this structure. Lichtenfels (1975) recognized extra-chitinous supports only in the genus *Cyathostomum* (which included the species now in *Coronocyclus*). Hartwich (1986) identified this structure in all members of the Cyathostominea, and used differences in its shape and attachments to surrounding structures to identify genera, including a new genus (*Coronocyclus*), in the tribe. He named the structure, ''support of the corona radiata externa'', and shortened the name to ''support''. Hartwich's (1986) descriptions of the support in all members of the Cyathostominea has made this character a standard part of the description of all species of the group and an important character for distinguishing genera and for determining relationships among them. The characteristic shape and attachments for the support in the various genera can be seen in Figs. 28, 40, 60, 66, 68, 72, 76, 80, 104, 108, 116, 120, 124 and 126.

Hartwich (1986) also described new details of the structure of the mouth collar that he found useful in the systematics of the Cyathostominea. He found two different forms of the structure of the mouth collar (previously noticed by Looss (1902): (1) the most common form, in which the ring of the collar is divided into inner and outer rings, is present (Hartwich, 1986) in all species of the genera *Cyathostomum*, *Cylicocyclus* (Fig. 80e) and *Cylicostephanus* and in *Cylicodontophorus bicoronatus* and (2) an undivided mouth collar, present in *Poteriostomum* and in a new genus,

Parapoteriostomum, erected by Hartwich (1986) for several species previously in the genus *Cylicodontophorus*.

Another characteristic of the mouth collar that Hartwich (1986) used to a greater extent than previous workers is the location of the posterior edge of the mouth collar in relation to the anterior edge of the buccal capsule. He found that the posterior edge of the mouth collar is located at about the same level as the anterior edge of the buccal capsule in all species of *Cyathostomum*, *Cylicocyclus*, *Cylicodontophorus* and *Poteriostomum*; posterior to it in *Cylicostephanus*; and far anterior to it in *Coronocyclus*.

The septum intracoronare was described by Hartwich (1986) as difficult to observe and not present in all species of the Cyathostominea. He described the structure as a septum bordering the posterior, or medial, edge of a pulpa in the mouth collar extending from the anterior edge of the buccal capsule, or the support, to a point on the lateral edge of the leaf crowns, varying among groups of species in the level it connects with the leaf crowns (Fig. 80e). He did find it useful, however, as a character for distinguishing species of the genera *Cyathostomum* (with a septum intracoronare) and *Coronocyclus* (without one); and for grouping species of *Cylicodontophorus* and a new genus, *Parapoteriostomum*, based on the attachment point of the septum intracoronare on the leaf crowns.

4. Methods

Collections of horse strongylids present in the US National Parasite Collection (USNPC) and in Schmalhauzen Institute of Zoology NAS of Ukraine (including specimens collected in Ukraine, Altay, Azerbaijan, Buryatia, Kazakhstan, Yakutia, Far East and other localities), and collections from The Natural History Museum (London), Muséum National d'Histoire Naturelle (Paris), South African Onderstepoort Museum (SAOM), Utrecht University, Zoological Museum of Berlin, Ohio State University, University of Glasgow and University of Liverpool.

Our comparative studies employed interference-contrast light microscopy of whole specimens cleared in phenol–alcohol solution (80% melted phenol crystals in 20% absolute ethanol). Drawings were prepared with the aid of a camera lucida. Photomicrographs were made with a digital camera, and halftone plates were prepared using Adobe Photoshop or Microsoft PowerPoint.

Phylogenetic analysis of a set of morphological characters was made with MacIntosh G-3 and G-4 computers and software including PAUP 4.0 and Mac Clade. Robustness of resulting trees was evaluated by application of differing methods for branch swapping and addition sequence; and through bootstrapping and calculation of Bremer decay values. Character evaluation, host associations and biogeography were examined using Mac Clade.

5. Classification

5.1. Key to genera

(1)	a. BC globular or subglobular	2
	b. BC cylindrical, wider anteriorly or posteriorly, or with ring-like hoop-shaped thickening posteriorly	6
(2)	a. Dorsal gutter absent or button-like	3
	b. Dorsal gutter extends to anterior end of BC	4
(3)	a. BC with well-developed turned-up collar at posterior end. Esophageal teeth do not extend to BC	*Oesophagodontus* (Strongylinae)
	b. BC wider anteriorly. One dorsal, blade-shaped and two sublateral, spear-shaped esophageal teeth extend into BC	*Bidentostomum* (Strongylinae)
(4)	a. BC subglobular, definitely longer than wide, its length more than 450 μm	*Strongylus* (Strongylinae)
	b. BC globular, its length less than 250 μm	5
(5)	a.Three large teeth composed of two plates joined at an angle medially extend into buccal cavity from esophageal funnel; elements of ELC numerous.	*Triodontophorus* (Strongylinae)
	b. ELC consists of six to eight broad elements	*Craterostomum* (Strongylinae)
(6)	a. Anterior end of esophagus greatly dilated, with three large sickle-shaped teeth	*Gyalocephalus* (Cyathostominae)
	b. Anterior end of esophagus not greatly dilated, sometimes with teeth which can extend into BC	7
(7)	a. Cylindrical BC greatly elongated, two to three times longer than wide	8
	b. BC not more than twice as long as wide	9
(8)	a. ELC consists of eight triangular elements. Dorsal gutter well-developed	*Caballonema* (Cyathostominae)
	b. ELC consists of six very modified elements. Dorsal gutter button-like	*Cylindropharynx* (Cyathostominae)
(9)	a. Esophageal teeth in invagination in dorsal sector of esophageal funnel. Elements of ELC narrow and long. Elements of ILC fused	*Tridentoinfundibulum* (Cyathostominae)
	b. The invagination on dorsal side of esophageal funnel absent. ELC and ILC well-developed. ILC can be poorly distinguished	10

(10)	a. Elements of ILC shorter, usually more numerous than elements of ELC	11
	b. Elements of ILC similar in length or longer than elements of ELC and equal or less numerous	16
(11)	a. Walls of BC thin concave or straight, with prominent ring-like thickening at base. Amphids, usually large and wide, project above MC surface	*Cylicocyclus* (Cyathostominae)
	b. Walls of BC definitely thick, without prominent ring-like thickening at base. Amphids usually do not project above MC surface	12
(12)	a. Insertion point of elements of ILC about 1/4–1/2 of BC depth. Elements of ILC similar to elements of ELC. Support of ELC well-developed	13
	b. Insertion point of elements of ILC about 1/4 or less of BC depth. Elements of ILC different from elements of ELC. Support of ELC poorly developed	14
(13)	a. Support for ELC continuous with BC, elongate, curving, thin at one end. Insertion line formed by posterior edge of elements of ILC curved or sinuous	*Cyathostomum* (Cyathostominae)
	b. Support for ELC separate from BC, elongate, spindle-shaped. Insertion line formed by posterior edge of elements of ILC straight	*Coronocyclus* (Cyathostominae)
(14)	a. Walls of BC straight, thicker posteriorly but without ring-like thickening at base. ELC consists of more than 25 elements	*Petrovinema* (Cyathostominae)
	b. Walls of BC shaped differently from a (above). ELC consists of 8–18 elements	15
(15)	a. Walls of BC have approximately equal thickness for entire length or slightly thicker anteriorly. Dorsal ray of male copulatory bursa has three branches	*Cylicostephanus* (Cyathostominae)
	b. Walls of BC much thicker anteriorly. Dorsal ray of male copulatory bursa has two branches	*Skrjabinodentus* (Cyathostominae)
(16)	a. Number of elements in ILC and ELC equal	17
	b. Number of elements in ILC less than in ELC	18
(17)	a. Walls of BC have approximately equal thickness throughout length. Insertion point of ILC at 1/4 of BC depth	*Cylicodontophorus* (Cyathostominae)
	b. Walls of BC thin, with small ring-like thickening at base. Insertion point of ILC at anterior end of BC depth	*Hsiungia* (Cyathostominae)
(18)	a. Walls of BC thick, gradually thicken posteriorly; approximately 1/4 shorter dorsally than ventrally. Dorsal ray of male copulatory bursa bifurcated only to most distal branch	*Poteriostomum* (Cyathostominae)
	b. Walls of BC thicken anteriorly; approximately equal length dorsally and ventrally. Dorsal ray of male copulatory bursa bifurcated to proximal branch	*Parapoteriostomum* (Cyathostominae)

5.2. Strongylinae

5.2.1. Strongylus Müller, 1780

Synonyms. Sclerostomata Rudolphi, 1809; *Sclerostoma* (Rud.): Blainville, 1828; *Sclerostomum* Dujardin, 1845; *Alfortia* Railliet, 1923; *Delafondia* Railliet, 1923.

General. Large Strongylinae. MC inflated, high, ring-shaped, divided into inner and outer rings. Posterior edge of MC posterior to anterior edge of BC. Amphids not markedly projected through MC surface. Only tips of submedian papillae extend through MC. Tips of submedian papillae cone-shaped, round or oval, short. Elements of ELC less numerous and markedly longer than those of ILC. Elements of ELC longer than broad, tip pointed; insertion point on tips of ILC. Elements of ILC longer than broad, tips pointed; insertion point on anterior edge of BC. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC surrounds anterior edge of BC, helmut-like. Septum intracoronare origin on BC. Medial insertion of septum intracoronare at junction of ELC and ILC. Walls of BC concave, thicker posteriorly, but without ring-like thickening. Buccal cavity oval, deeper than wide. Dorsal gutter elongate, more than 1/2 depth of BC. Buccal teeth present or absent. Esophageal funnel shallow. Esophageal teeth not prominent. Anterior muscular portion of esophagus about 1/4–1/3 of esophagus length. Excretory pore markedly anterior to NR, in region of buccal capsule. Deirids at level of NR.

Male. Dorsal ray with six branches. Ventral rays shorter than laterals. Dorsal lobe shorter then lateral lobes. Externodorsal rays origin on stem of dorsal rays. Gubernaculum small, straight, with ventral groove. Genital cone short, conical. Spicule tips straight or slightly curved.

Female. Vulva two to three, or more, tail lengths from anus. Vagina shorter than ovejector sphincters. Ovejector vestibule T-shaped, infundibula shorter than sphincters. Tail conical, short, less than 2× diameter at anus.

Type species. *S. equinus* Müller, 1780

5.2.2. Key to species of Strongylus

(1) a. Prominent teeth present in buccal cavity	2
b. Teeth absent from buccal cavity	*S. edentatus*
(2) a. Dorsal and ventral teeth present in buccal cavity; dorsal tooth single with two points; two ventral teeth pointed and shorter than dorsal tooth	*S. equinus*
b. Only bilobed dorsal tooth present	3
(3) a. Lobes of tooth high, rounded, smooth; extend nearly one-half depth of BC. Excretory pore near nerve ring. Dorsal lobe of copulatory bursa longer than lateral lobes	*S. vulgaris*
b. Lobes of tooth low, flat, grooved; extend less than one-third depth of BC. Excretory pore at level of BC. Dorsal lobe of copulatory bursa equal to or shorter than lateral lobes	*S. asini*

5.2.3. *S. equinus* Müller, 1780 (Figs. 2 and 6a)

Synonyms. *Strongylus equorum* Zeder, 1800; *Strongylus armatus* Rudolphi, 1802, in part; *Strongylus neglectus* Poeppel, 1897; *Sclerostoma equinum* (Müller, 1780) Blainville, 1828; *Sclerostomum quadridentatum* Sticker, 1901, not Dujardin, 1845.

General. ELC less numerous (40–56) and longer than ILC (42–80). Dorsal and ventral teeth present in buccal cavity; dorsal tooth single with two points; two ventral teeth pointed and shorter than dorsal tooth.

Male. Body length 24–36 mm. Esophagus length 1.80–1.98 mm. BC width 880–990 mm; depth 1.02–1.23 mm. Spicule length 2.75–3.18 mm. Gubernaculum length 328–431.[2] Dorsal ray length 475–497. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone variable. Studied specimens have two fingerlike protrusions. Protrusions of dermal collar absent.

Female. Body length 39–46 mm. Esophagus length 1.9–2.5 mm. BC width 1.11–1.26; depth 1.12–1.42. Vulva to tail tip 11.5–14.5 mm. Anus to tail tip 1.03–1.90 mm. Egg size 71–90 × 42–55.

Hosts. *E. caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

5.2.4. *S. asini* Boulenger, 1920 (Figs. 3 and 6c)

Synonyms. *Delafondia asini* (Boulenger, 1920) Skrjabin, 1933.

General. ELC and ILC resembling those of *S. equinus*. Only bilobed dorsal tooth present in buccal cavity. Lobes of tooth low, flat, grooved; extend less than one-third depth of BC. Deirids near middle of glandular esophagus, 1.5 mm from anterior end.

Male. Body length 18–32 mm. Esophagus length 1.6–2.4 mm. BC width 970–990; depth 840–890. Dorsal lobe of copulatory bursa equal to or shorter than lateral lobes. Spicule length 1.6–1.9 mm. Gubernaculum length 376–384. Dorsal ray length 608–688. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone poorly developed. Protrusions of dermal collar absent.

Female. Body length 30–42 mm. Esophagus length 1.65–2.6. BC width 1.19–1.26 mm; depth 90–910. Vulva to tail tip 6.0–7.0 mm. Anus to tail tip 400–600. Egg size 61–66 × 37–46.

Hosts. *E. asinus*, *E. burchelli*, *E. zebra hartmannae*.

Locality. Cecum, colon.

Distribution. Africa, Asia, North America.

5.2.5. *S. edentatus* (Looss, 1900) Railliet and Henry, 1909 (Figs. 4 and 6b)

Synonyms. *Sclerostoma edentatum* Looss, 1900; *Alfortia edentatus* (Looss, 1900) Skrjabin, 1933.

General. Teeth absent from buccal cavity. Elements of ELC markedly less numerous (55–75) than ILC (80) and about same length.

Male. Body length 22–26 mm. Esophagus length 1.65–1.80 mm. BC width 800–857; depth 734–840. Spicule length 1.9 mm. Gubernaculum length 340–380. Dorsal ray length 520–536. Genital cone elongated with appendages. Dermal collar well-developed on ventral side of genital cone. Two pairs of appendages of genital cone well-developed: first pair wide, nipple-shaped; second pair longer with fine processes.

Female. Body length 32–43 mm. Esophagus length 1.9–2.2 mm. BC width 1.02–1.19 mm; depth 1.02–1.20. Vulva to tail tip 9–10 mm. Anus to tail tip 120–200. Egg size 90–98 × 43–51.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

5.2.6. *S. vulgaris* (Looss, 1900) Railliet and Henry, 1909 (Figs. 5 and 6d)

Synonyms. *Sclerostoma vulgare* Looss, 1900; *Strongylus armatus* Rudolphi, 1802, in part; *Sclerostomum bidentatum* Sticker, 1901; *Delafondia vulgaris* (Looss, 1900) Skrjabin, 1933.

[2] Here and below measurements are given in micrometers if other is not stated.

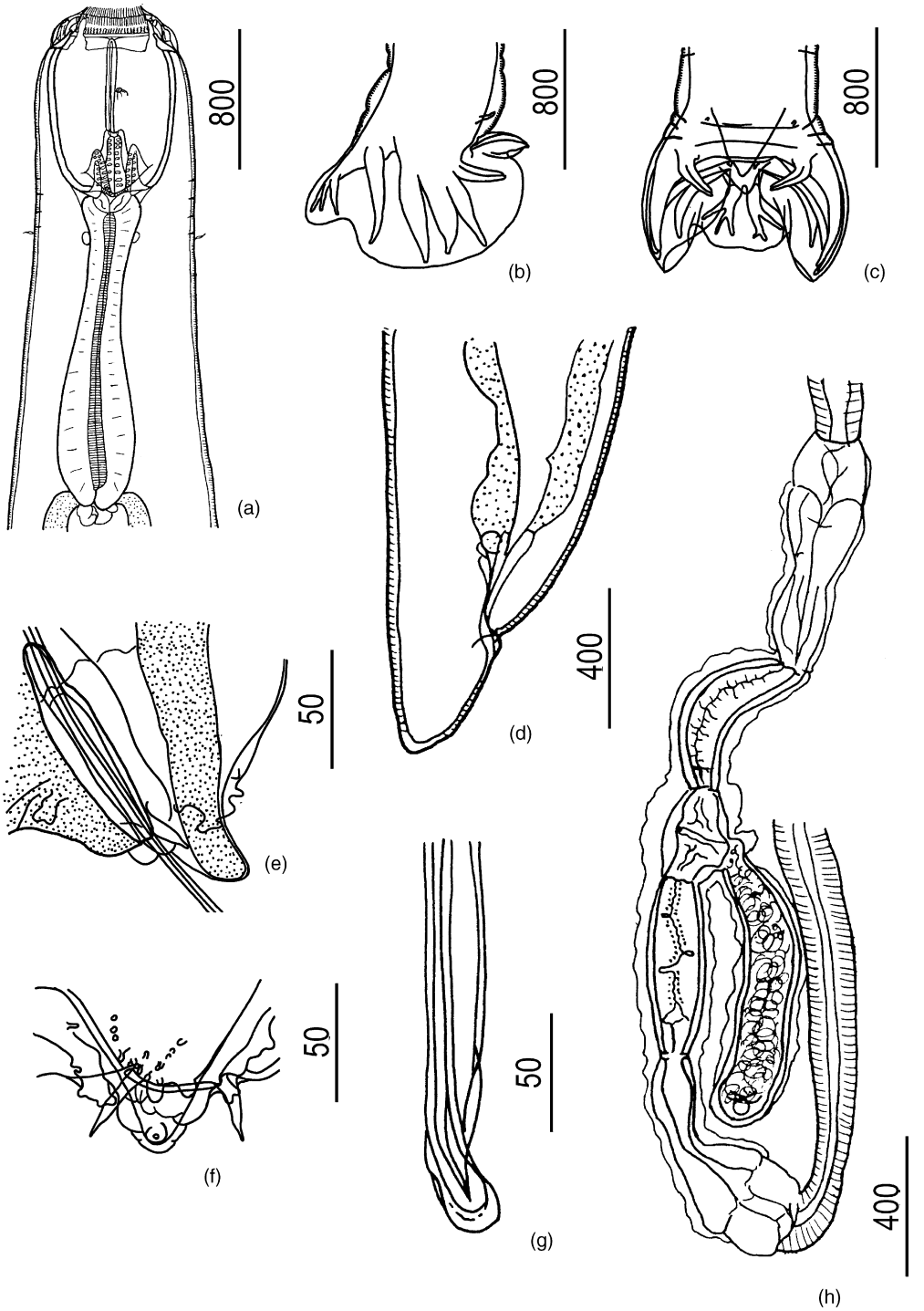

Fig. 2. *Strongylus equinus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male. (h) Ovejectors and vagina, lateral view (from Dvojnos and Kharchenko, 1994).

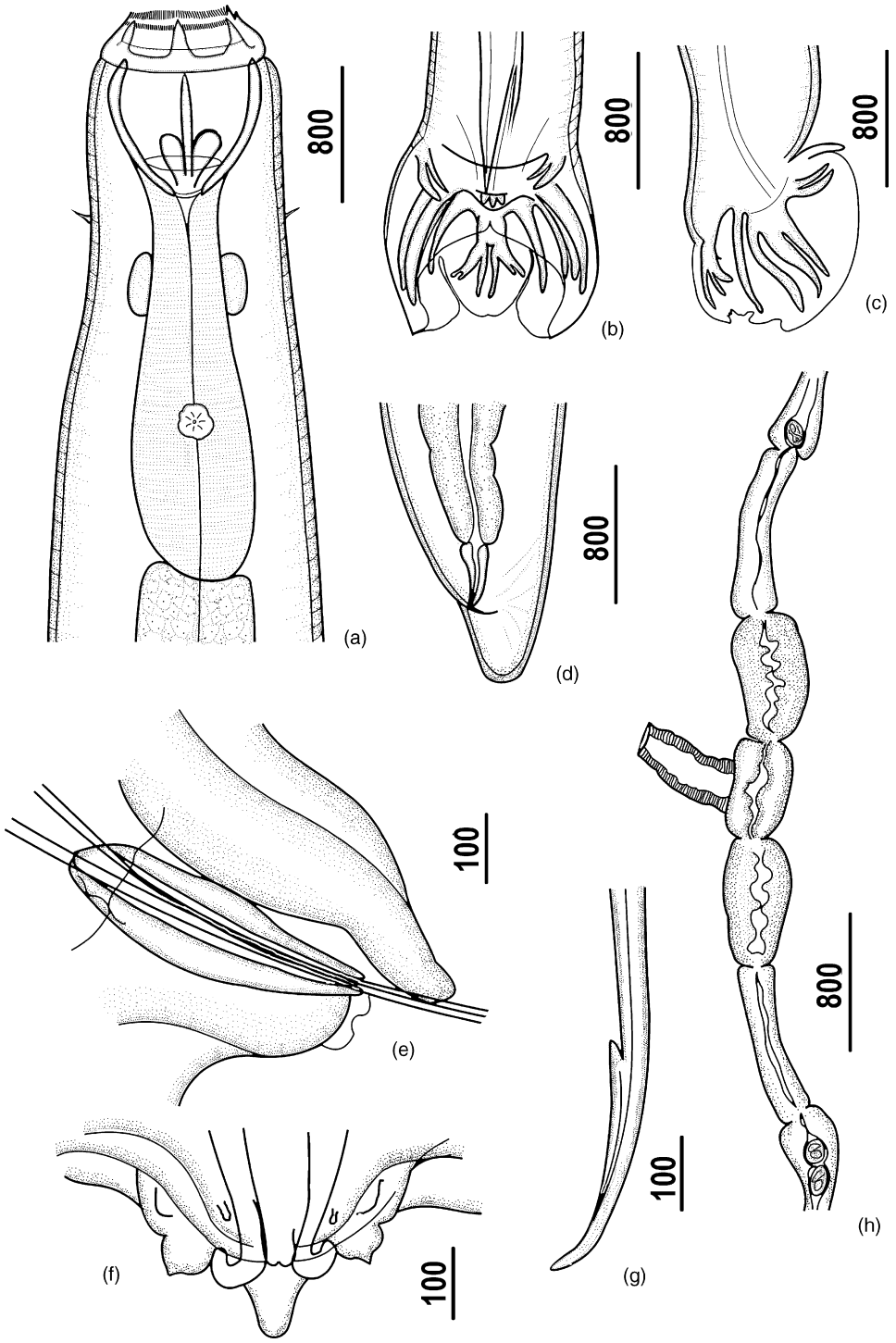

Fig. 3. *Strongylus asini*. (a) Esophageal region, ventral view. (b) Male tail, dorsoventral view. (c) Male tail, lateral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male. (h) Ovejectors and vagina, lateral view.

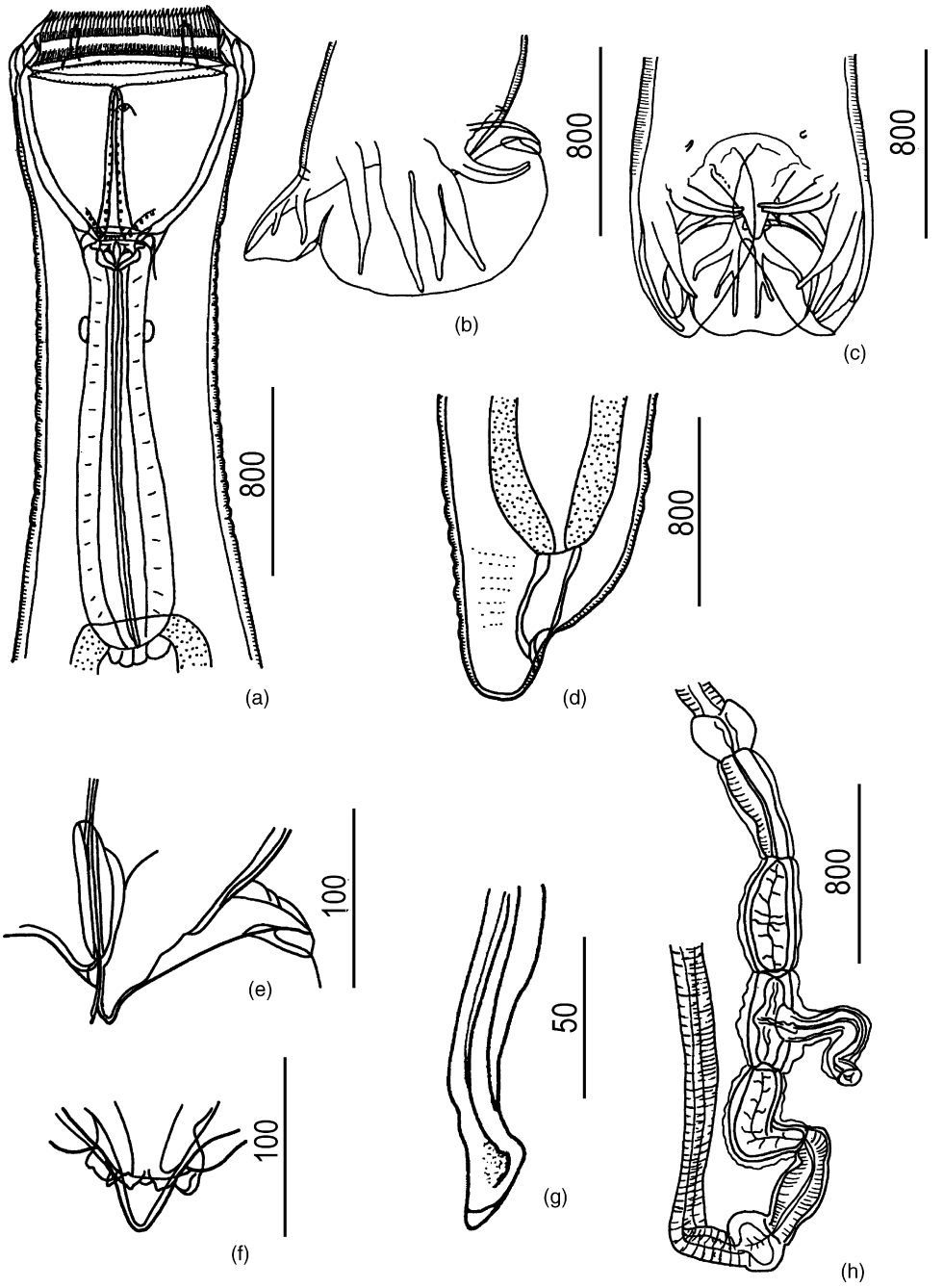

Fig. 4. *Strongylus edentatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male. (h) Ovejectors and vagina, lateral view (from Dvojnos and Kharchenko, 1994).

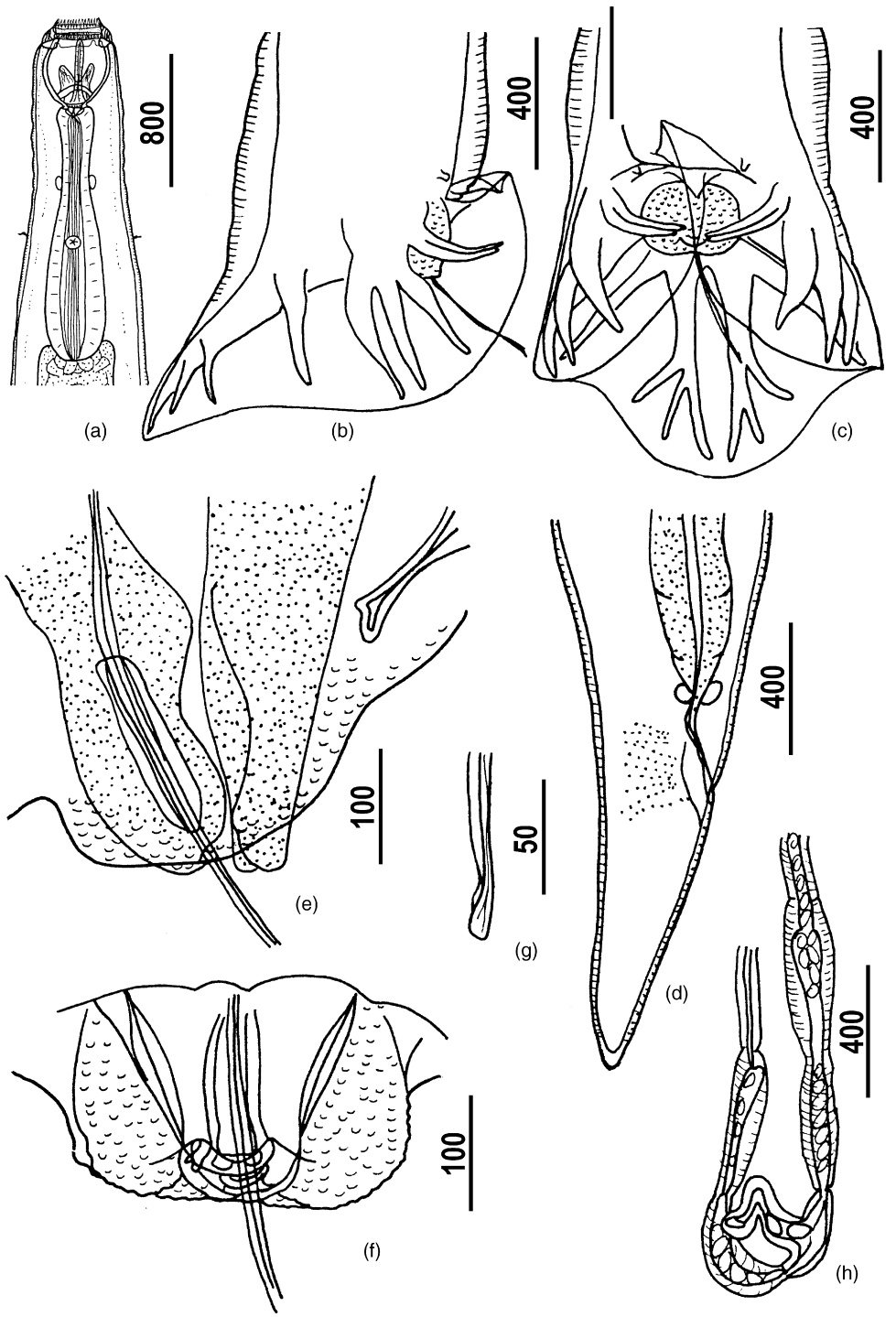

Fig. 5. *Strongylus vulgaris*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. g. Fused spicule tips of male. (h) Ovejectors and vagina, lateral view (from Dvojnos and Kharchenko, 1994).

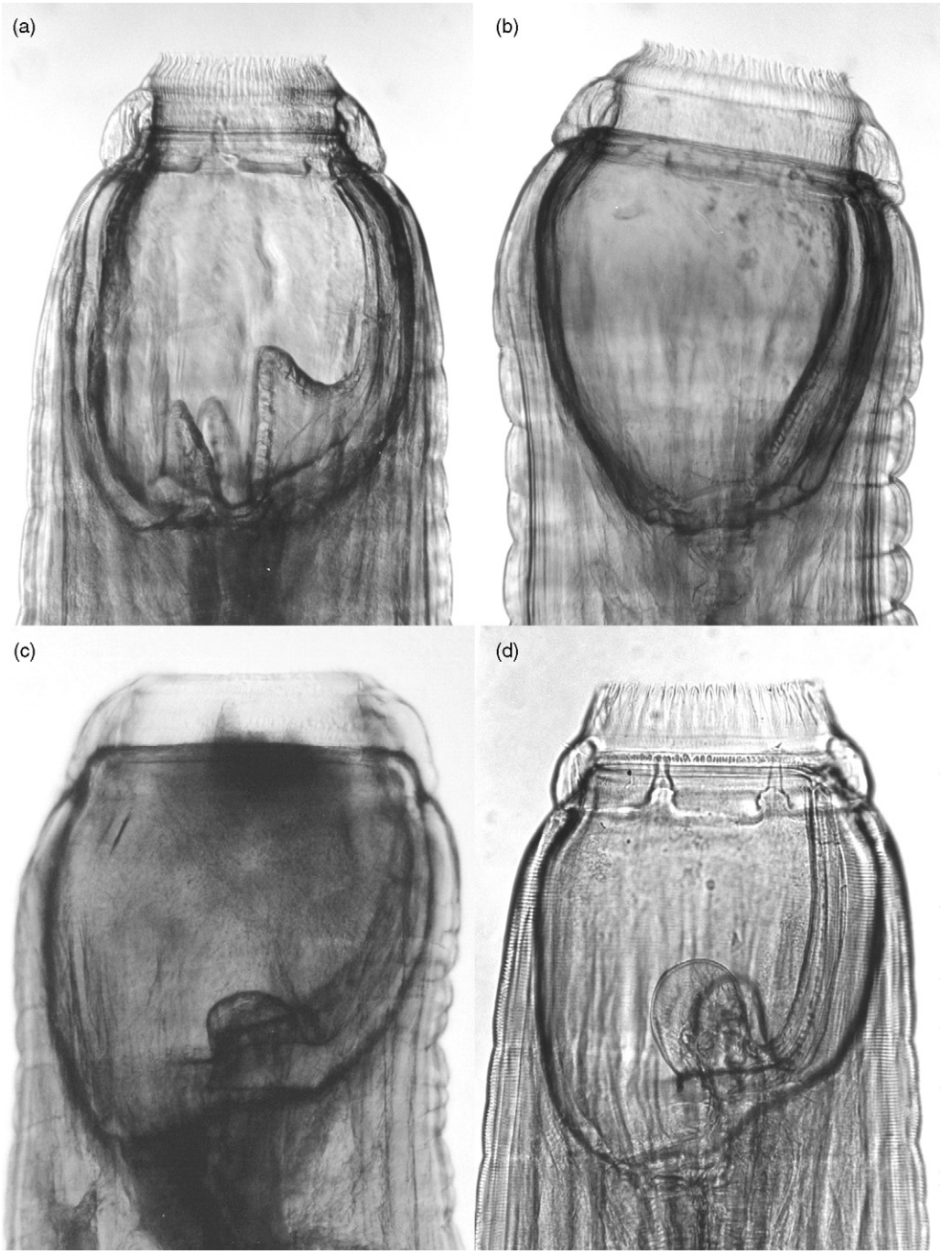

Fig. 6. Heads of different *Strongylus* species, lateral view. (a) *S. equinus*. (b) *S. edentatus*. (c) *S. asini*. (d) *S. vulgaris*. (b and d from Lichtenfels, 1975).

General. ELC numerous; ILC less distinguished. Only bilobed dorsal tooth present. Lobes of tooth high, rounded, smooth; extend nearly one-half depth of BC. Deirids near middle of glandular esophagus; 1.45–1.60 mm from anterior end.

Male. Body length 14.5–16.0 mm. Esophagus length 1.3–1.4 mm. BC width 480–500; depth 560–610. Dorsal lobe of copulatory bursa longer than lateral lobes. Spicule length 2.1–2.4 mm. Gubernaculum length 220. Dorsal ray length 580–610. Dermal collar poorly developed. Cuticle of genital cone with small round thickenings. Protrusions of dermal collar absent.

Female. Body length 20.0–24.0 mm. Esophagus length 1.5–1.6 mm. BC width 552–650; depth 480–690. Vulva to tail tip 6.0–7.1 mm. Anus to tail tip 0.8–1.0 mm. Egg size 67–75 × 40–46.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

5.2.7. Discussion

Looss (1900) recognized, in *Sclerostomum* (following Rudolphi, 1809; Diesing, 1851), two new species, *S. edentatus* and *S. vulgaris*, among specimens of *S. equinus*. Railliet and Henry (1909) reestablished *Strongylus* for these species. A fourth species, *S. asini*, was described from donkeys, *Equus asinus*, from East Africa by Boulenger (1920). The four species were grouped by Railliet (1923) in three subgenera (*Strongylus (Strongylus) equinus*, *S. (Alfortia) edentatus* and *S. (Delafondia) vulgaris* and *S. (D.) asini*), which were raised to generic level by Skrjabin (1933). More recently, most workers followed Lichtenfels (1975, 1980) in placing all four species in *Strongylus*, without recognizing *Alfortia* or *Delafondia* even at subgenus level. However, several experts on these nematodes have continued to recognize *Alfortia* and *Delafondia* either at the genus level (Popova, 1955; Dvojnos and Kharchenko, 1994; Zhang and K'ung, 2002) or the subgenus level (Hartwich, 1994). The recognition of *Alfortia* and *Delfondia* has been based on differences in buccal teeth and dorsal rays of males. When included in the analysis, *S. asini* has been included in *Delafondia* with *S. vulgaris* because of the similar buccal tooth structure. This opinion was based on different life cycles, L3 morphology, pathology and convenience in naming disease syndromes. However, Boulenger (1920) considered *S. asini* to be more similar to *S. edentatus* and *S. equinus* in characteristics of the female and male tails and in having an excretory pore at the level of the buccal capsule (near the nerve ring in *S. vulgaris*). Hung et al. (1996) found the ITS-2 sequence of *S. asini* to be more similar to those of *S. edentatus* (87.1%) and *S. equinus* (95.3%) than to that of *S. vulgaris* (73.9%). This result supports the retention of the four species within one genus. Thus, because of a lack of congruent morphological characters for subdividing *Strongylus*, we prefer to follow the simplest, most commonly used, taxonomy for these four similar species.

5.3. *Oesophagodontus* Railliet and Henry, 1902

Synonyms. *Pseudosclerostomum* Quiel, 1919.

General. Large Strongylinae. Mouth collar depressed with sharp ridge on peripheral edge, undivided. Posterior edge of MC anterior to anterior edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae very long, about four or more times as long as thick, uniform thickness. Stalk of submedian papillae broader than long, with short bilobed process. Elements of ELC markedly less numerous than those of ILC and about same length. Elements of ELC longer than broad, tips pointed; insertion point on tips of ILC. Numerous elements of ILC longer than broad, tips pointed; ILC elements are bent backwards at base with free ends reflected slightly anteriorly; insertion point on anterior edge of BC. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, elongate, curving, thin at one end. Septum intracoronare origin on support. Medial insertion of septum intracoronare situated anterior to junction of ELC and ILC. Walls of BC concave, with thickened posterior ring. Buccal cavity funnel-shaped, wider anteriorly; wider than deep. Dorsal gutter inconspicuous. Buccal teeth absent. Esophageal funnel moderately enlarged. Esophageal teeth prominent. Anterior muscular portion of esophagus about $^1/_4$–$^1/_3$ of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches; medial fissure wide, extends to base of lobe. Ventral rays shorter than laterals. Dorsal lobe shorter then lateral lobes. Externodorsal rays origin on stem of dorsal rays. Gubernaculum small, straight, with ventral groove. Genital cone short, conical. Spicule tips straight or slightly curved.

Female. Vulva two to three, or more, tail lengths from anus. Vagina shorter than sphincter of ovejector. Ovejector vestibule broadly Y-shaped, infundibulum about equal to sphincter. Tail conical, long, more than 2× diameter at anus.

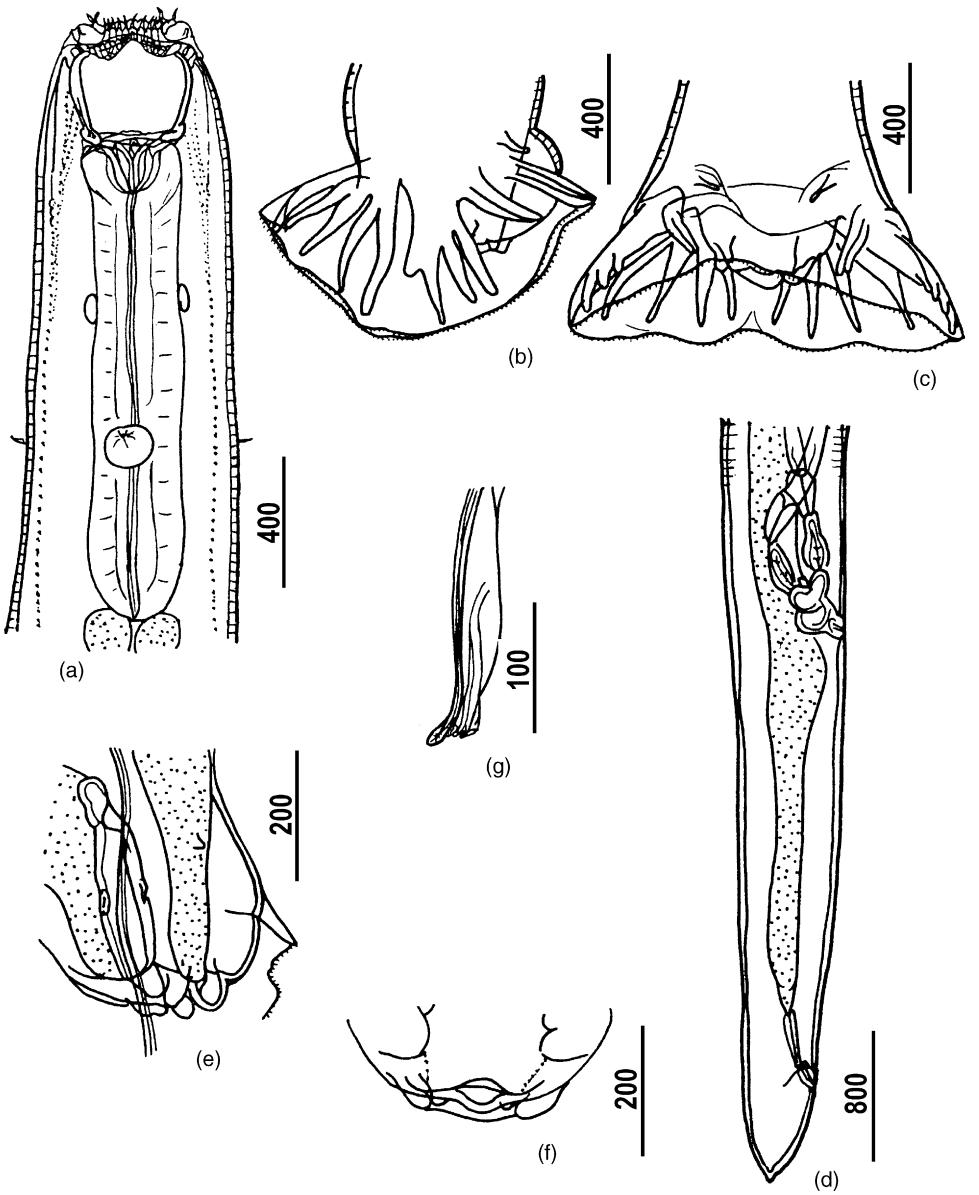

Fig. 7. *Oesophagodontus robustus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (from Dvojnos and Kharchenko, 1994).

Type species. *O. robustus* (Giles, 1892) Railliet and Henry, 1902

5.3.1. O. robustus (Giles, 1892) Railliet and Henry, 1902 (Figs. 7 and 8)

Synonyms. *Sclerostoma robustum* Giles, 1892; *Pseudosclerostomum securiferum* Quiel, 1919; *Strongylus robustus* (Giles, 1892) Popov, 1927.

General. With characteristics of the genus. Elements of ELC markedly less numerous (18) than those of ILC (34–48) and about same length.

Male. Body length 15.0–20.0 mm. Esophagus length 0.9–1.7 mm. BC width 320–470, depth 220–320. Spicule length 620–765. Gubernaculum length 269–320. Dorsal ray length 328–367. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone two paired, thick finger-shaped projections.

Female. Body length 19.0–24.0 mm. Esophagus length 1.6–1.8 mm. BC width 425–490, depth 323–450. Vulva to tail tip 2.2–3.5. Anus to tail tip 500–700. Egg size 88–130 × 40–60.

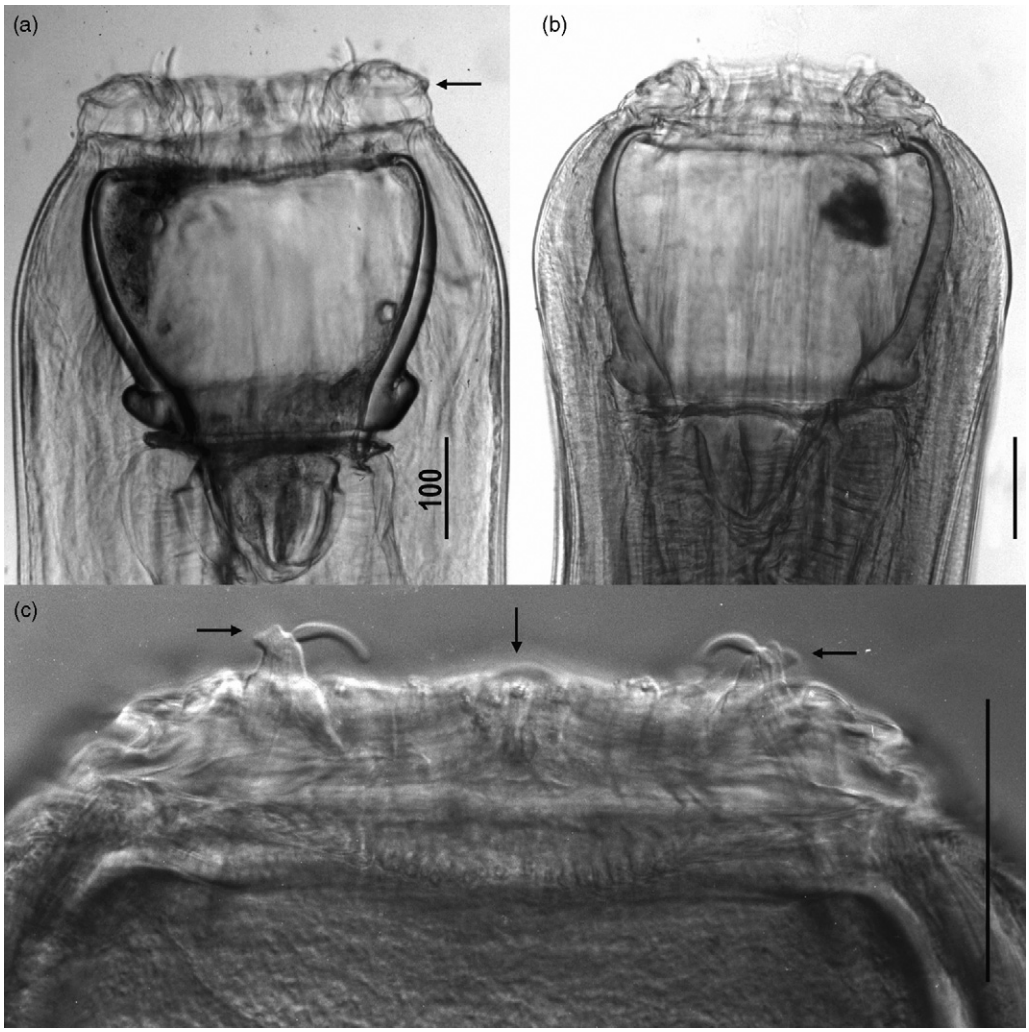

Fig. 8. *Oesophagodontus robustus*. (a) Buccal capsule, dorsoventral view. Arrow marks amphid or lateral papilla. (b) Buccal capsule, lateral view. (c) Mouth collar, lateral view, showing two submedian papillae, each with short bilobed process on stalk (horizontal arrows) and long slender tip, and lateral papilla (vertical arrow).

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

5.3.2. Discussion

The only species in this genus was described by Giles (1892) as *Sclerostoma robustum* from horses and mules in India. Later it was moved to a new genus, *Oesophagodontus*, by Railliet and Henry (1902). *Oesophagotontus*. *robustus* is a rare but cosmopilitan species. It was found by Boulenger (1916) in horses in England, by Turner (1920) in zebra in an English Zoo, by Theiler, 1924 in a horse and a mule in South Africa, by Popov (1927) in horses of Russia and by other authors. Theiler, 1924 noted that the species is very rare in South Africa, only three females were found: one in a horse and two in a mule. As *Pseudosclerostomum securiferum* it was described by Quiel (1919).

Larvae of third stage *O. robustus* have 18 triangular intestinal cells. Recently many authors around the world reported this species in coprological examinations (Mirzayans et al., 1974; Colglazier et al., 1977; Ambrosi, 1981 and others), and, Eydal (1983) found nine nematode genera, including *Oesophagodontus robustus*, in faecal samples but not during post mortem examinations. Thus, *O. robustus* may not be as rare as previously believed.

5.4. *Craterostomum* Boulenger, 1920

General. Small Strongylinae. MC flattened, divided into inner and outer rings. Posterior edge of MC posterior to anterior edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae bullet-shaped, round or oval, short. Stalk of submedian papillae longer than broad. Number of elements of ELC less numerous and longer than elements of ILC. Elements of ELC as long as broad, tips pointed; insertion point on tips of ILC. Elements of ILC as broad as long, tips pointed; insertion point at 1/4 or less of BC depth. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC surrounds anterior edge of BC, short, triangular in optical section. Septum intracoronare origin on support. Medial insertion of septum intracoronare situated at junction of ELC and ILC. Walls of BC concave, thicker anteriorly. Buccal cavity wider posteriorly, wider than deep. Dorsal gutter elongate, more than 1/2 depth of BC. Buccal teeth absent. Esophageal funnel moderately enlarged. Esophageal teeth prominent. Anterior muscular portion of esophagus about 1/4–1/3 of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches. Ventral rays shorter than laterals. Dorsal lobe longer then lateral lobes. Externodorsal rays origin on stem of dorsal rays. Gubernaculum with small handle, enlarged distal tip. Genital cone short, conical. Spicule tips straight or slightly curved.

Female. Vulva more than one tail length from anus. Vagina shorter than sphincter. Ovejector vestibule oval or Y-shaped, infundibulum about equal to sphincter. Tail conical, long, more than 2× diameter at anus.

Type species. *C. acuticaudatum* (Kotlán, 1919) Ihle, 1920

Species inquirenda. *Craterostomum tenuicauda* Boulenger, 1920; *Craterostomum tenuicauda*, of Rai (1960).

5.4.1. *C. acuticaudatum (Kotlán, 1919) Ihle, 1920 (Figs. 9 and 10)*

Synonyms. *Cylicostomum acuticaudatum* Kotlán, 1919; *Cylicostomum mucronatum* Ihle, 1920; *Craterostomum mucronatum* (Ihle, 1920) Ihle, 1920.

General. With characteristics of the genus. Elements of ELC markedly longer and less numerous than ILC (8 against 23–24).

Male. Body length 5.7–9.9 mm. Esophagus length 390–486. BC width 70–94, depth 45–58. Distance from deirids to head end 255–260, from excretory pore 327–332. Spicules length 620–766. Gubernaculum length 165–204. Dorsal ray length 333–347. Ventral rays shorter than laterals. Dermal collar well-developed on genital cone. Appendages of genital cone two fingerlike protrusions fused medially. Protrusions of dermal collar absent.

Female. Body length 6.8–10.6 mm, length of esophagus 420–528, width of BC 70–94, depth 45–57, distance from deirids to head end 260, distance from vulva to tail tip 1.2–1.28 mm, from anus to tail tip 402–563, egg size 120 × 60.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchell*, *E. zebra hartmannae*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

5.4.2. *Discussion*

Lichtenfels (1975) reviewed the history of this genus and the three species proposed. He agreed with Skrjabin and Ershov (1933) and most subsequent workers that *C. mucronatum* is a synonym of *C. acuticaudatum*. However, the status of *C. tenuicauda* is not so clear. The original description of *C. tenuicauda* was of females only and they were immature. Most workers (Popova, 1955) subsequently regarded this species to be a synonym of *C. acuticaudatum*. However, Rai (1960) redescribed *C. tenuicauda* from mature females and males from a pony collected in India, separating it from *C. acuticaudatum* on the basis of a different number of ILC and ELC elements (18 and 9, compared with 22–26 and 6–8 in *C. acuticaudatum*), a proportionately shorter tail although the body length is greater, and the presence of submedian cephalic papillae that are not notched. Rai's description of the female tail and his drawing of it do not agree with each other and are thus questionable. Neither the tail of Rai's females nor the unnotched character of the submedian papillae agree with the Boulenger's (1920) description of *C. tenuicauda* or with the generic diagnosis of *Craterostomum*. The status of *C. tenuicauda*, of Boulenger, 1920 and of *C. tenuicauda*, of Rai, 1960, which are unlikely to be conspecific based on differences in the morphology of the females, are uncertain and need further study. We consider *C. tenuicauda* Boulenger, 1920 to be a species inquirenda. Rai's (1960) specimens should not be considered to be *C. tenuicauda*. They may represent an undescribed species, but discrepancies in the description prevent consideration of its status until specimens can be studied.

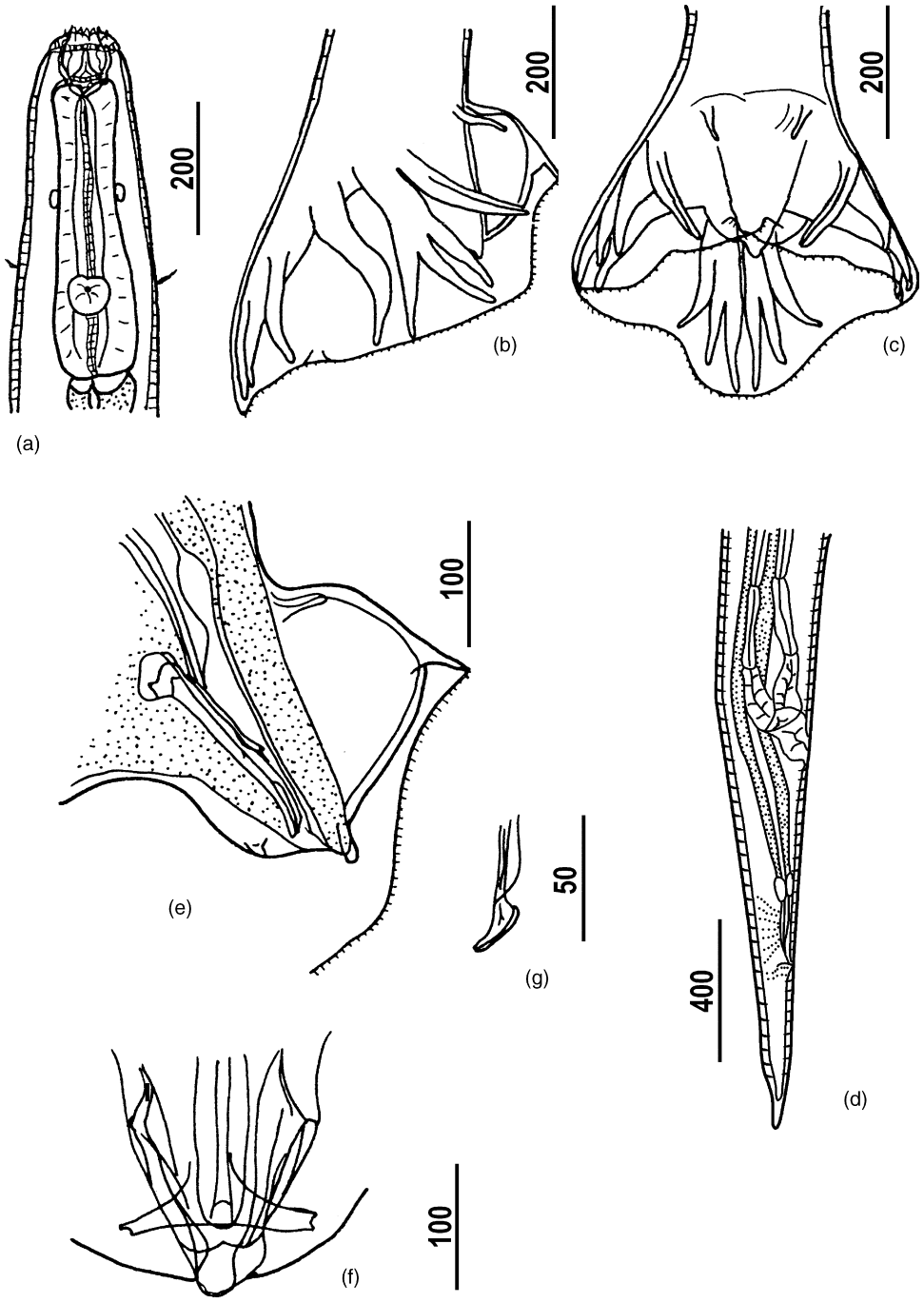

Fig. 9. *Craterostomum acuticaudatum*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (from Dvojnos and Kharchenko, 1994).

5.5. *Bidentostomum Tshoijo, in Popova (1958)*

General. Small-sized Strongylinae. MC flattened, divided into inner and outer rings. Posterior edge of MC posterior to edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae bulbous, two to three times as long as thick. Stalk of submedian papillae broader than long. Elements of ELC markedly less numerous but equal in

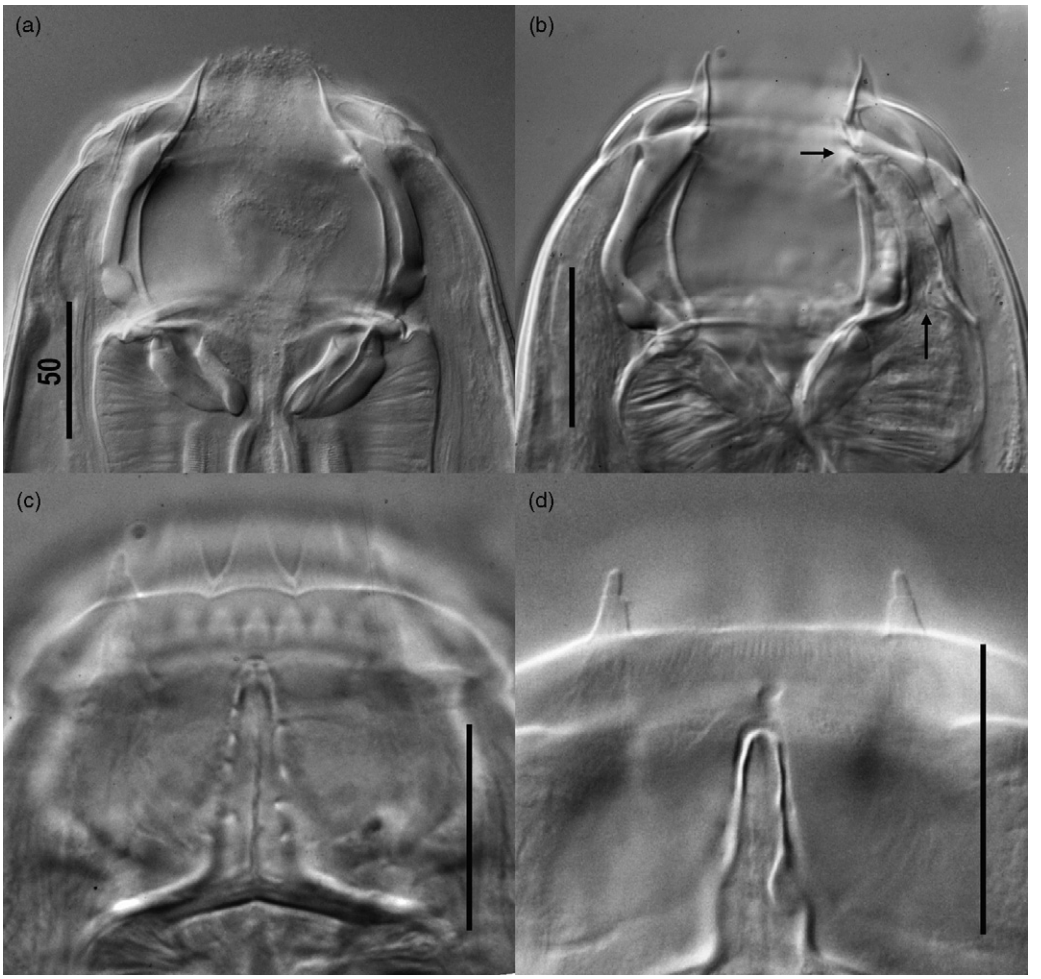

Fig. 10. *Craterostomum acuticaudatum*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing dorsal gutter (arrows). (c) Elements of ELC and ILC and dorsal gutter, dorsal view. (d) Submedian papillae and dorsal gutter.

length to ILC elements. Elements of ELC as long as broad, tip pointed; insertion point on support. Elements of ILC longer than broad, tips pointed; insertion point at 1/5 or less of BC depth. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC surrounds anterior edge of BC, short, triangular in optical section. Septum intracoronare origin on support. Medial insertion of septum intracoronare situated anterior to junction of ELC and ILC. Walls of BC concave, thicker anteriorly. Buccal cavity wider posteriorly, wider than deep. Dorsal gutter nipple- or button-like. Buccal teeth absent. Esophageal funnel shallow. Large esophageal teeth extend into BC for most of its depth. Anterior muscular portion of esophagus about $^1/_4$–$^1/_2$ of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches. Ventral rays equal to laterals. Dorsal lobe longer then laterals. Externodorsal rays origin at junction of dorsal and lateral lobes. Gubernaculum elongate, narrow with small handle, enlarged distal tip and ventral notch near proximal end. Genital cone elongate, extends beyond bursal edge. Spicule tips hook- or harpoon-shaped.

Female. Vulva more than one tail length from anus. Vagina longer than sphincter. Ovejector vestibule oval or Y-shaped, infundibulum about equal to sphincter. Tail conical, long, length more than twice diameter at anus.

Type species. *B. ivaschkini* Tshoijo in Popova (1958)

5.5.1. *B. ivaschkini Tshoijo in Popova (1958) (Figs. 11 and 12)*

General. With characteristics of the genus. 8 elements in ELC; 16 in ILC. ELC and ILC equal in length.

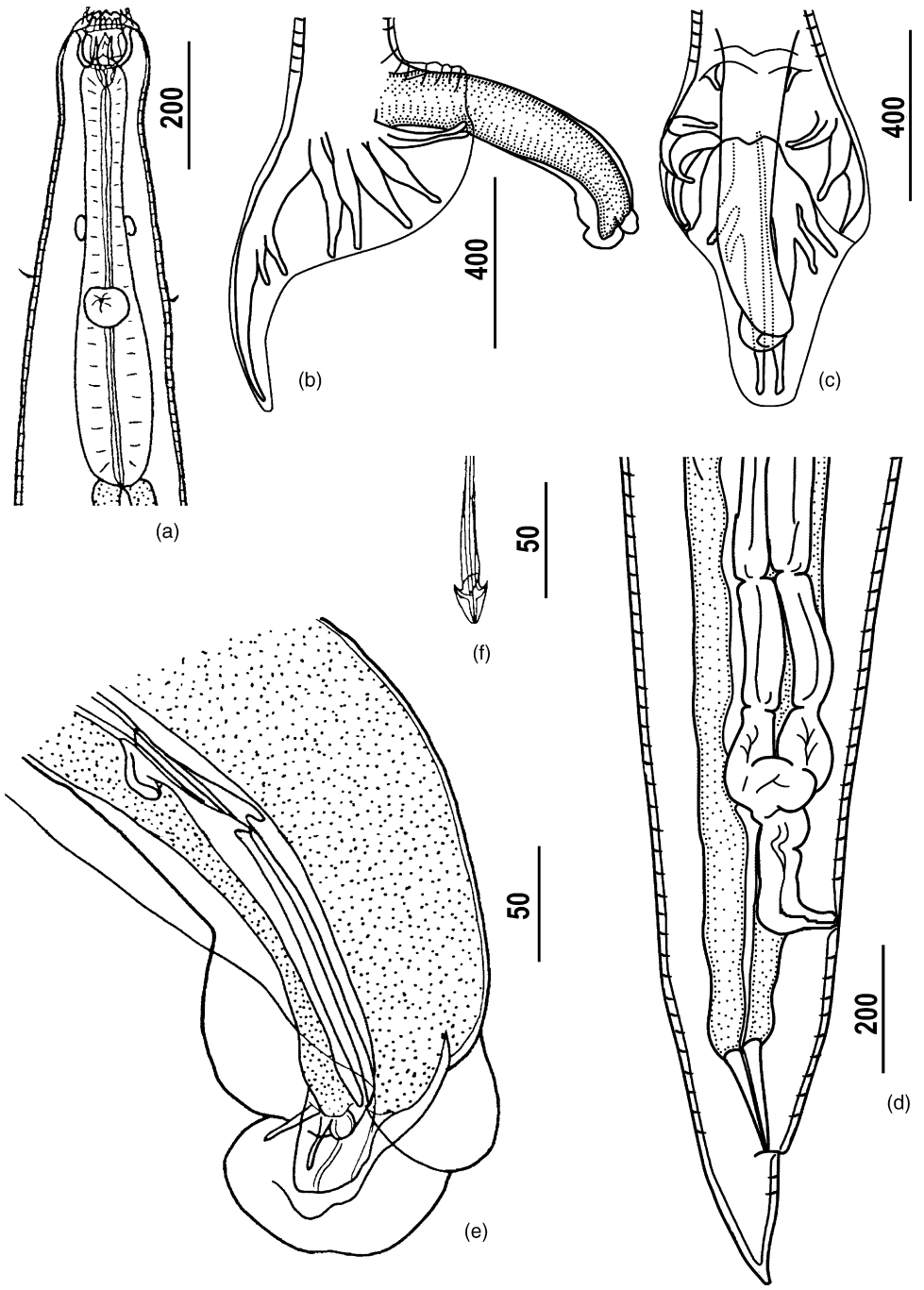

Fig. 11. *Bidentostomum ivashkini*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Fused spicule tips of male (from Dvojnos and Kharchenko, 1994).

Male. Body length 8.0–9.0 mm. Esophagus length 560–640. BC width 56–75, depth 54–65. Distance from excretory pore to head end 415–498, Spicules length 830–890. Gubernaculum length 174–208. Dorsal ray length 680–710. Ventral and lateral rays equal in length. Dermal collar undeveloped. Edges of bursa smooth. Appendages of genital cone consist of two finger-like projections.

Female. Body length 9.0–10.0 mm, length of esophagus 380–451, Width of BC 63–83; depth 53–66.

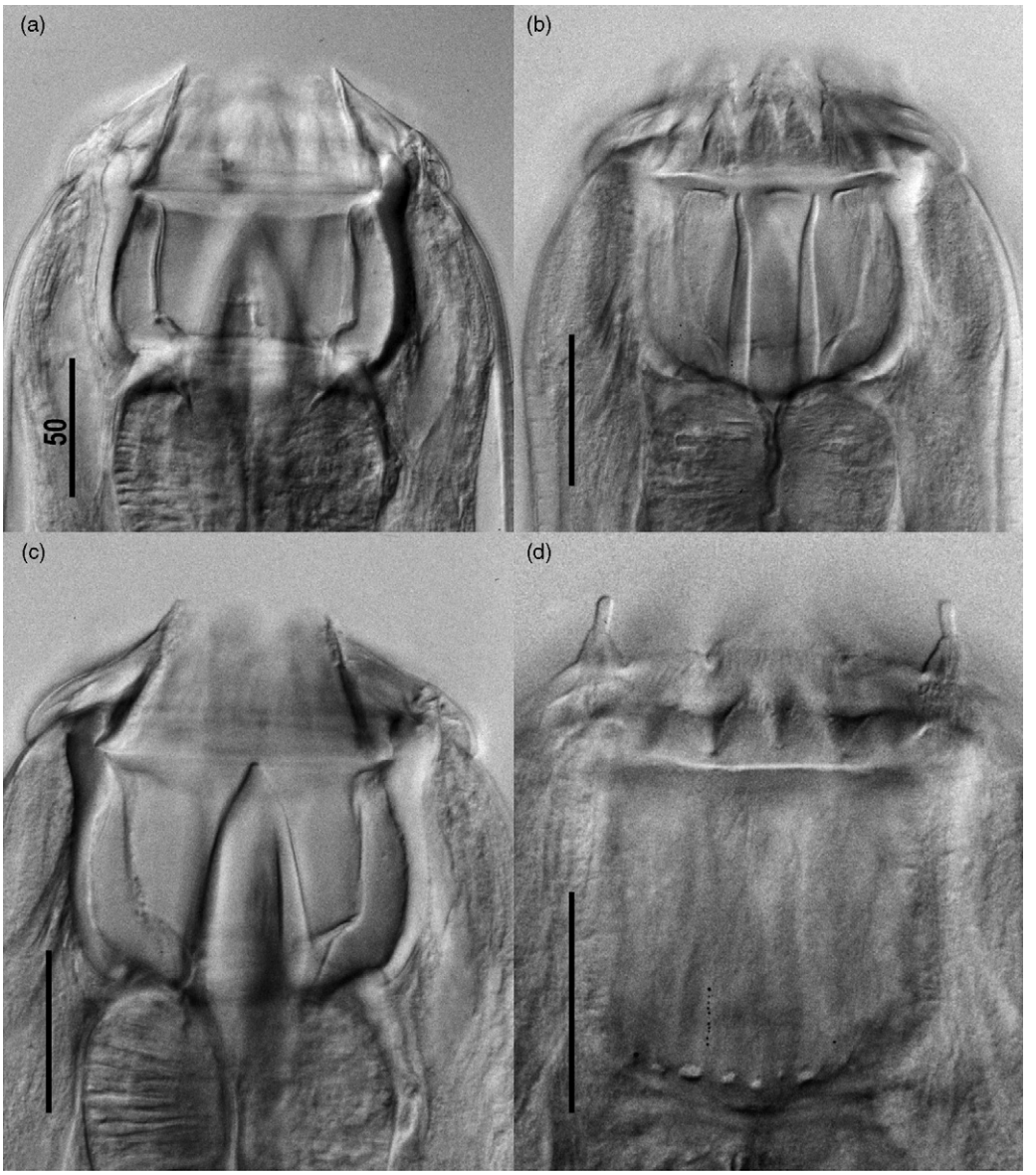

Fig. 12. *Bidentostomum ivashkini*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, ventral view, showing two long, slender subventral esophageal teeth and elements of ILC and ELC. (c) Buccal capsule, dorsal view, showing large dorsal esophageal tooth. (d) Submedian papillae and elements of ILC.

Distance from excretory pore to head end 457–498. Vulva to tail tip 542–747. Anus to tail tip 216–299. Egg size 101–107 × 51–52.

Hosts. *Equus caballus*, *E. caballus* × *E. asinus*.

Locality. Cecum, colon.

Distribution. Asia.

5.5.2. Discussion

Tshoijo in his dissertation (Tschoijo, 1957) described *Bidentostomum ivaschkini*, a strikingly unique strongylid from three Mongolian horses and a mule. The description and figures were published in (Popova, 1958) and in a separate article (Tshoijo, 1959). Because of the unusual configuration of the buccal teeth of *B. ivaschkini* and the unconventional classification employed by Tshoijo, Lichtenfels (1975) considered this nematode to be of uncertain classification. After studying types of *B. ivaschkini* in Moscow in 1978, Lichtenfels (1980) recognized the validity of this genus and placed it in the Strongylinae.

The species was redescribed by Ivashkin and Dvojnos (1984) and Dvojnos and Kharchenko (1994). *Bidentostomum ivaschkini* is the only species in the genus and it has been collected only in Mongolia (Tshoijo, 1959; Ulambayar, 1988), Kazakhstan (Dementiev, 1964; Kosupko and Nechinennyi, 1983; Dvojnos and Kharchenko, 1994).

5.6. *Triodontophorus (Looss, 1900) Looss, 1902*

Synonyms. *Triodontus* Looss, 1900.

General. Medium-sized Strongylinae. MC inflated, ring-shaped or flattened with sharp outer edge divided into inner and outer rings. Posterior edge of MC posterior to anterior edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae cone-shaped, two to three times as long as thick. Stalk of submedian papillae longer than broad. Elements of ELC equal in number and longer than elements of ILC. Elements of ELC longer than broad, tip pointed; insertion point on tips of ILC. Elements of ILC plate-like, slightly longer than broad, tip rounded; insertion point on anterior edge of BC. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC surrounds anterior edge of BC, helmut-like. Septum intracoronare origin on support. Medial insertion of septum intracoronare situated anterior to junction of ELC and ILC. Walls of BC concave, thicker anteriorly and posteriorly. Buccal cavity oval. Dorsal gutter elongate, more than 1/2 depth of BC. Buccal teeth absent. Esophageal funnel shallow. Esophageal teeth extend into BC. Anterior muscular portion of esophagus about 1/4–1/2 of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches. Ventral rays shorter than laterals. Dorsal lobe equal to, or longer than, lateral lobes. Externodorsal rays originate at junction of dorsal and laterals. Gubernaculum with large, dorsal handle and ventral notch. Genital cone short, conical. Spicule tips hook- or harpoon-shaped.

Female. Vulva more than one tail length from anus. Vagina shorter or longer than sphincter. Ovejector vestibule oval or Y-shaped; infundibulum shorter than sphincter. Tail conical, short (1× diameter at anus) or long(more than 2× diameter at anus).

Type species. *T. serratus* (Looss, 1900) Looss, 1902

5.6.1. *Key to species of Triodontophorus*

(1)	a. Mouth collar appears in optical section as inflated round tube in ring around mouth; female tail long; vulva separated from anus by 1.5–3.0 mm; spicules more than 3.0 mm long	*T. serratus*
	b. Mouth collar somewhat flattened with acute edge around outside perimeter; female tail short; vulva separated from anus by less than 1.0 mm; spicules less than 2.0 mm long	2
(2)	a. Cuticle strongly serrated in cervical region; dorsal lobe of bursa short; teeth finely denticulated	*T. tenuicollis*
	b. Cuticle striated but relatively smooth; dorsal lobe of bursa long; teeth smooth or strongly denticulated	3
(3)	a. Submedian papillae short, broad, and conical; teeth usually smooth except for three elevations on each; dorsal lobe of bursa very long (625–800); female tail very short; vulva very close to anus	*T. brevicauda*
	b. Submedian papillae long, narrow, and pointed; dorsal lobe of bursa less than 600 long; female tail short; vulva separated from anus by more than twice tail length	4
(4)	a. Leaf-crowns consist of 44–50 elements; usually many small to medium irregular denticulations on each tooth	*T. minor*
	b. Leaf-crowns consist more than 55 elements; denticulations on teeth large, fine and regular or absent	5
(5)	a. Serrations on upper edge of teeth completely absent	*T. burchelli*
	b. Serrations on upper edge of teeth present in different forms	6
(6)	a. Usually three large denticulations on each lateral part of each tooth	*T. nipponicus*
	b. Medium serration of teeth	*T. hartmannae*

5.6.2. *T. serratus (Looss, 1900) Looss, 1902 (Figs. 13 and 14)*

Synonyms. *Triodontus serratus* Looss, 1900; *Triodontophorus intermedius* Sweet, 1909.

General. Mouth collar appears in optical section as inflated round tube in ring around mouth. Submedian papillae short, conical. Numbers of elements of ELC and ILC 48–56. Buccal cavity oval, slightly wider than deep. Upper edge of esophageal teeth serrated. Cuticle striated but relatively smooth.

Male. Body length 12–16 mm. Esophagus length 0.9–1.2 mm. BC width 140–152, depth 78–95. Distance from deirids to head end 720–730. Spicule length 3.0–3.45 mm. Gubernaculum length 348–392. Dorsal ray length 364–402. Dermal collar well–developed on

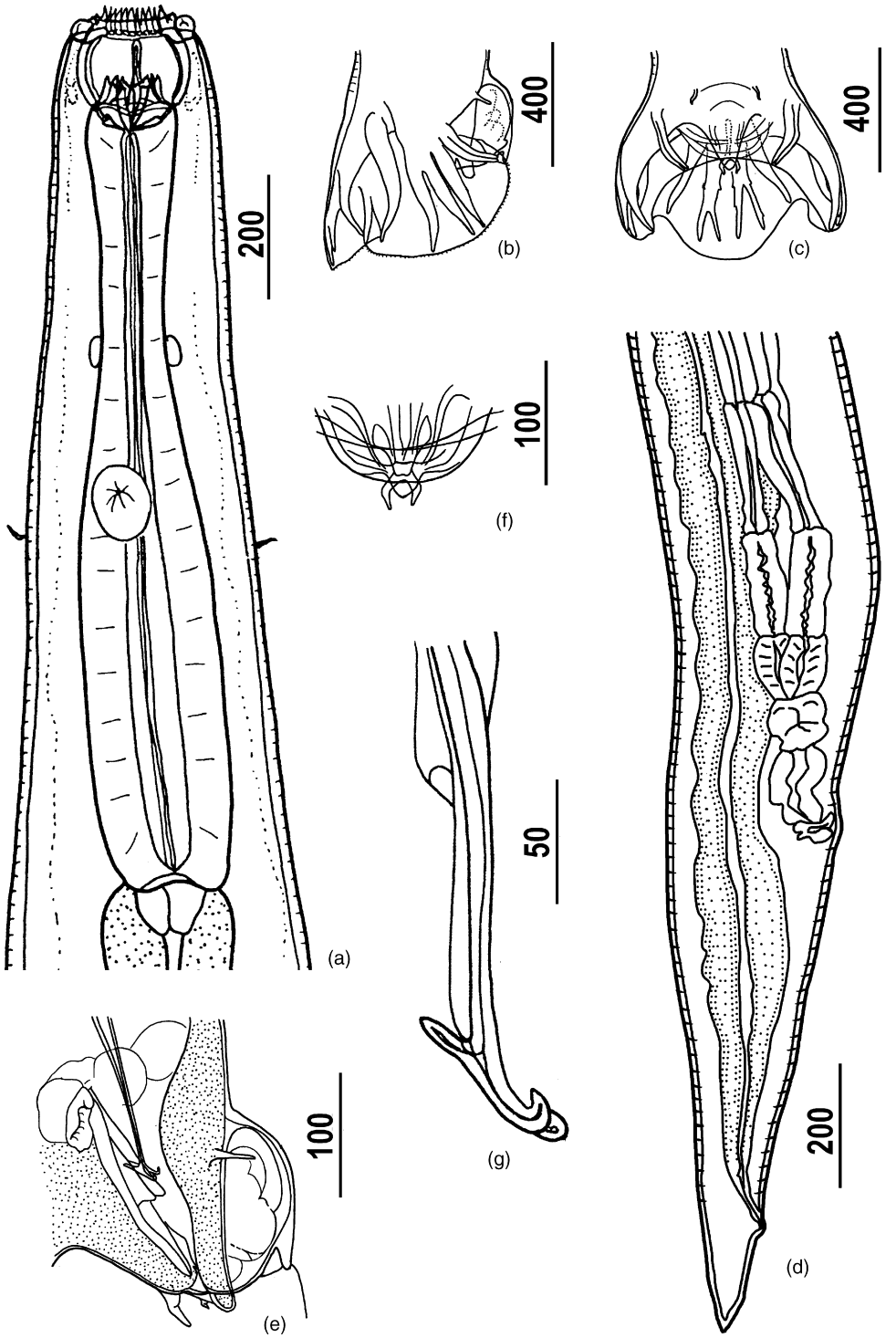

Fig. 13. *Triodontophorus serratus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

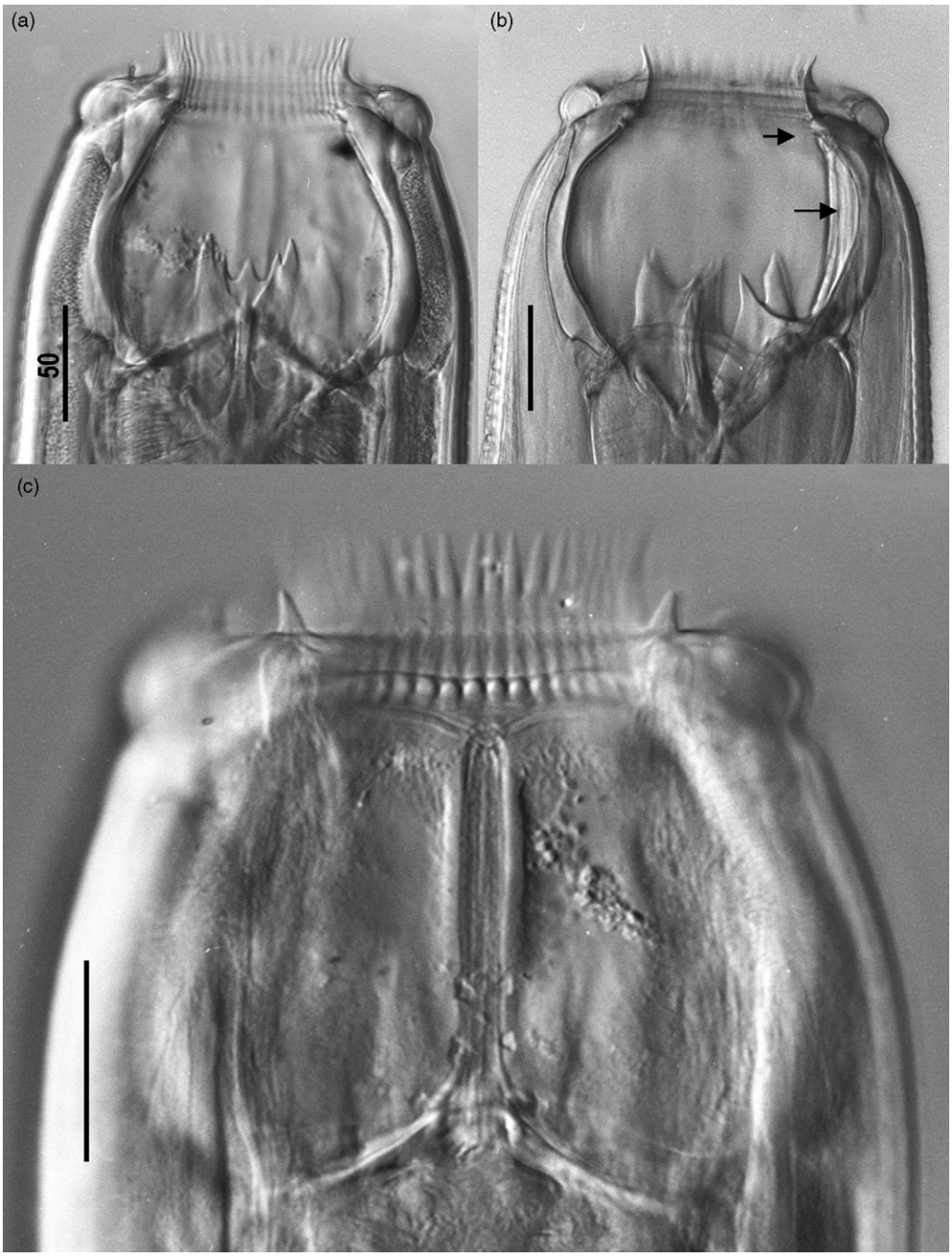

Fig. 14. *Triodontophorus serratus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. Arrows mark dorsal gutter. (c) Mouth collar, dorsal view, showing two submedian papillae, elements of ILC and ELC and dorsal gutter (a and c from Lichtenfels, 1975).

ventral side of genital cone. Appendages of genital cone two finger-shaped projections, the bases of which fuse behind cloaca. Protrusions of dermal collar absent.

Female. Body length 16–20 mm. Esophagus length 1.16–1.2 mm. BC width 172–189, depth 93–118. Deirids to head end 755–772.Vulva to tail tip 1.591–2.1. Anus to tail tip 367–658. Egg size 86–120 × 52–68.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

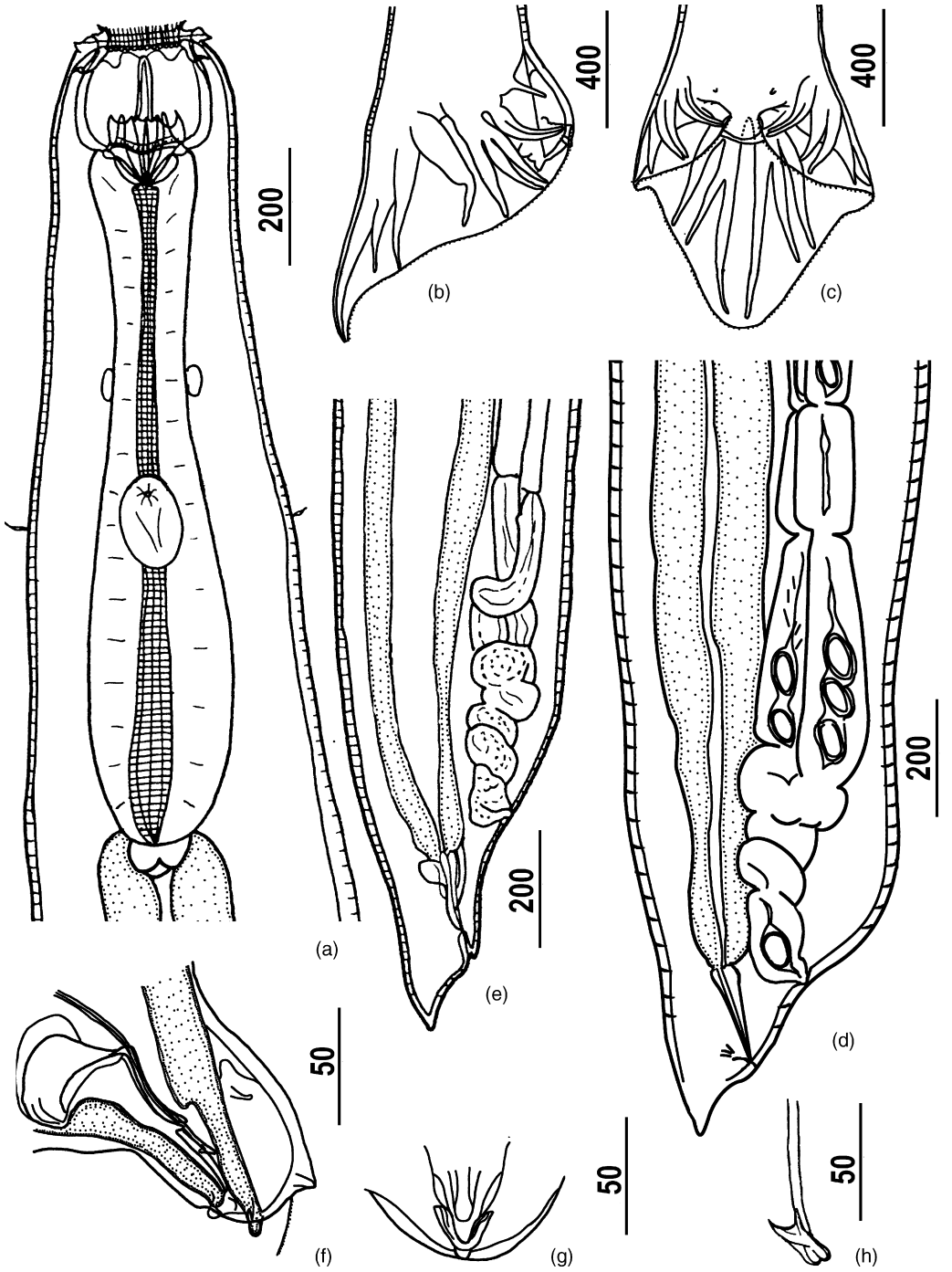

Fig. 15. *Triodontophorus brevicauda*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) and (e) Tails of females showing variations that may be due to maturity of specimen. (f) Genital cone, lateral view. (g) Tip of genital cone, ventral view. (h) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

5.6.3. T. brevicauda Boulenger, 1916 (Figs. 15 and 16)

General. Mouth collar flattened. Submedian papillae short, conical. ELC and ILC elements numerous, 61–68. Buccal cavity oval, as wide as deep. Upper edges of esophageal teeth not denticulated. Cuticle striated but relatively smooth.

Male. Body length 13.0–15.0 mm. Esophagus length 1.12–1.29 mm. BC width 172–210, depth 150–199. Spicule length 1.62–1.79 mm. Gubernaculum length

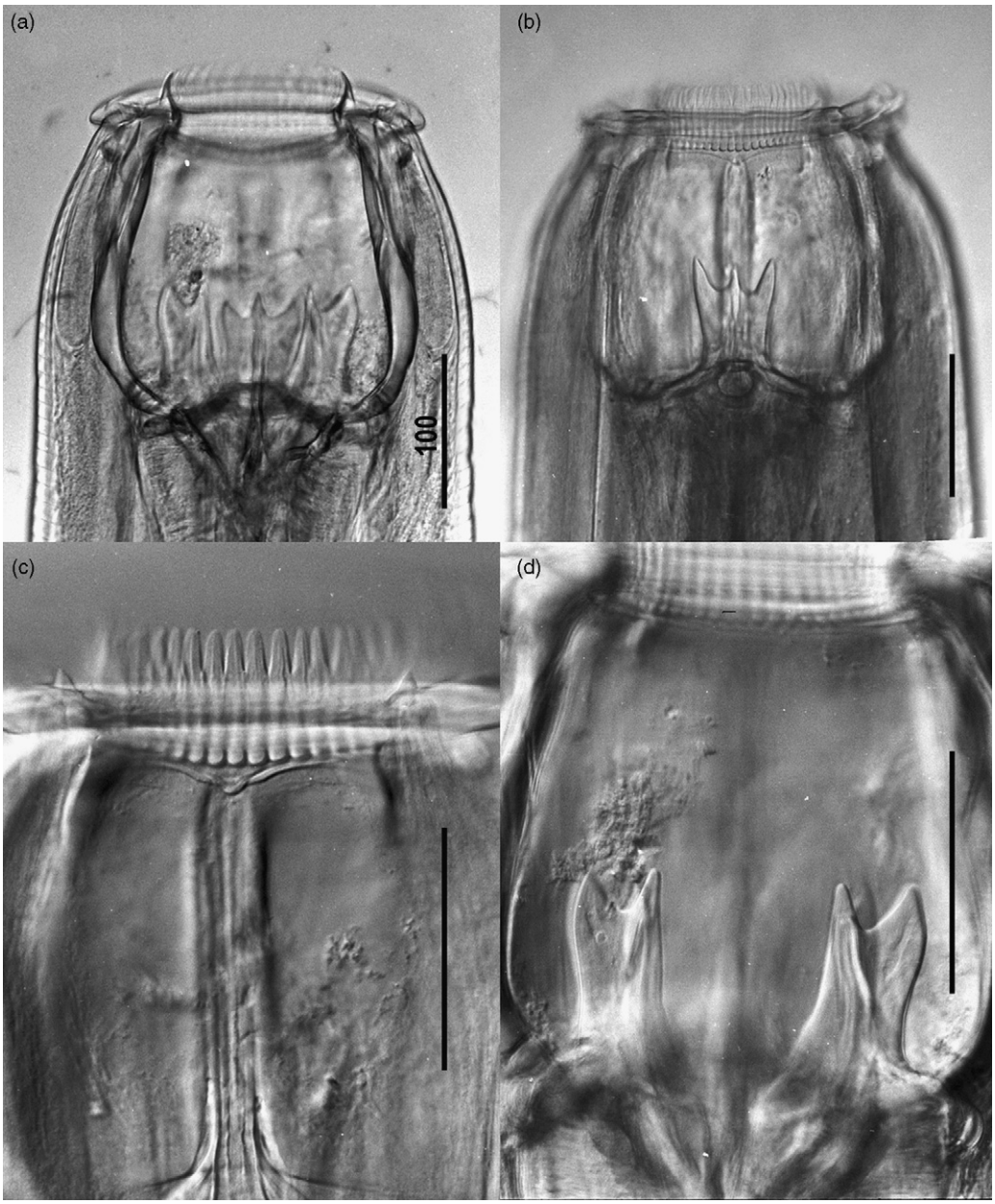

Fig. 16. *Triodontophorus brevicauda*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Mouth collar, lateral view, showing two submedian papillae, elements of ELC and ILC and dorsal gutter. (d) Two of three large esophageal teeth (b and c from Lichtenfels, 1975).

323–340. Dorsal ray length 723–796. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone inconspicuous, semispherical.

Female. Body length 14.5–19.2 mm. Esophagus length 1.1–1.2 mm. BC width 245–257, depth 260–283. Vulva to tail tip 268–328. Anus to tail tip 110–128. Egg size 85–102 × 44–56.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

5.6.4. *T. burchelli* Krecek et al., 1997 (Figs. 17 and 18)

General. Mouth collar flattened, with acute erect edge around outside perimeter. Submedian papillae long, narrow, and pointed. ELC and ILC elements number 60–61. Buccal cavity oval, as long as wide.

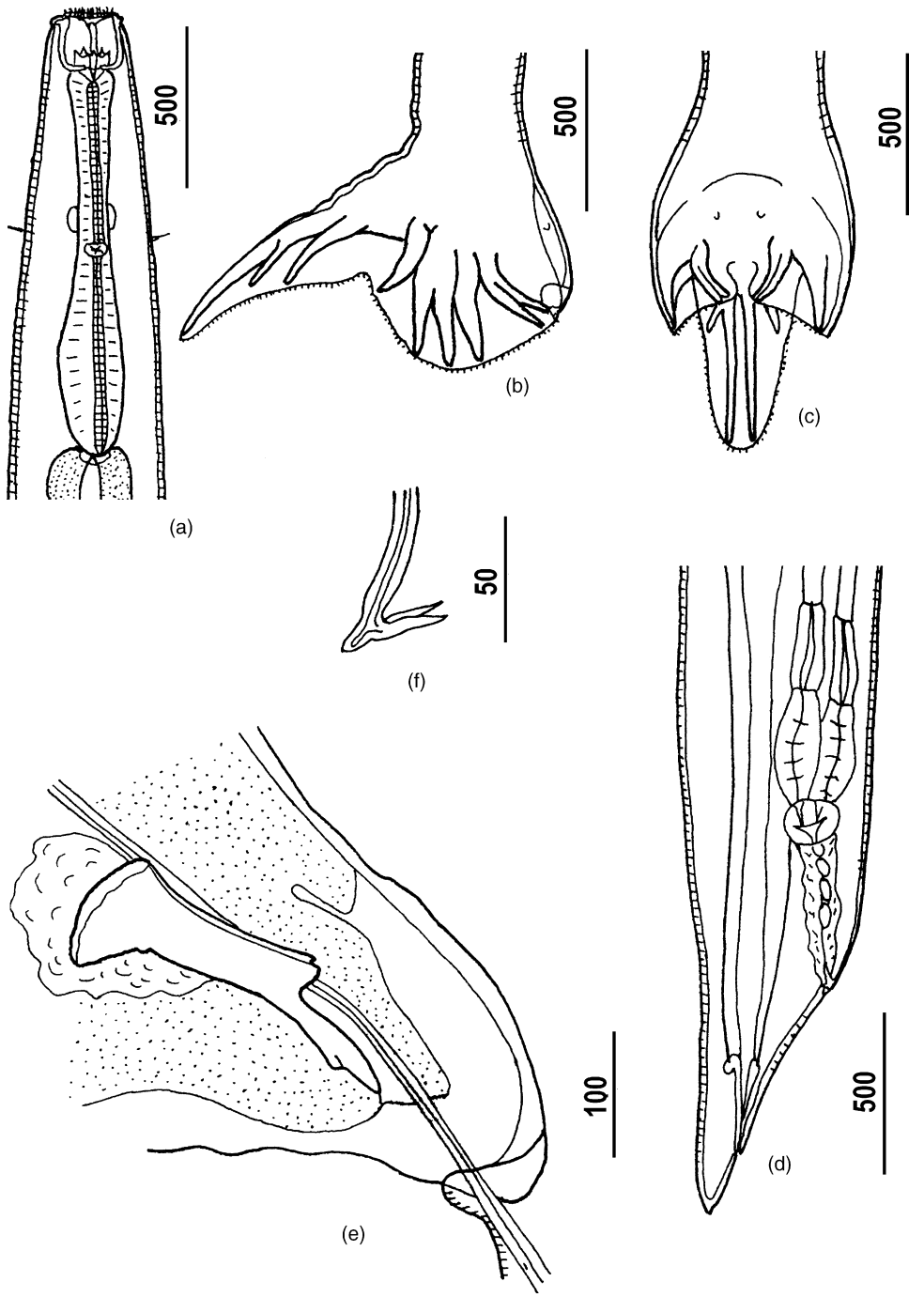

Fig. 17. *Triodontophorus burchelli*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (e) Fused spicule tips of male (modified from Krecek et al., 1997).

Upper edge of esophageal teeth without any serrations. Cuticle striated but relatively smooth.

Male. Body length 12.9–18.0 mm. Esophagus length 0.8–1.2 mm. BC width 120–153, depth 120–165. Anterior end to: deirids 638–904; excretory pore 510–788. Spicule length 1.5–2.2 mm. Gubernaculum length 224–285. Dorsal ray length 464–754. Dermal collar poorly developed on ventral side of genital cone. Appendages of genital cone inconspicuous.

Female. Body length 14.2–19.2 mm. Esophagus length 0.9–1.5 mm. BC width 129–210, depth 114–180. Anterior end to: deirids 742–962; excretory pore

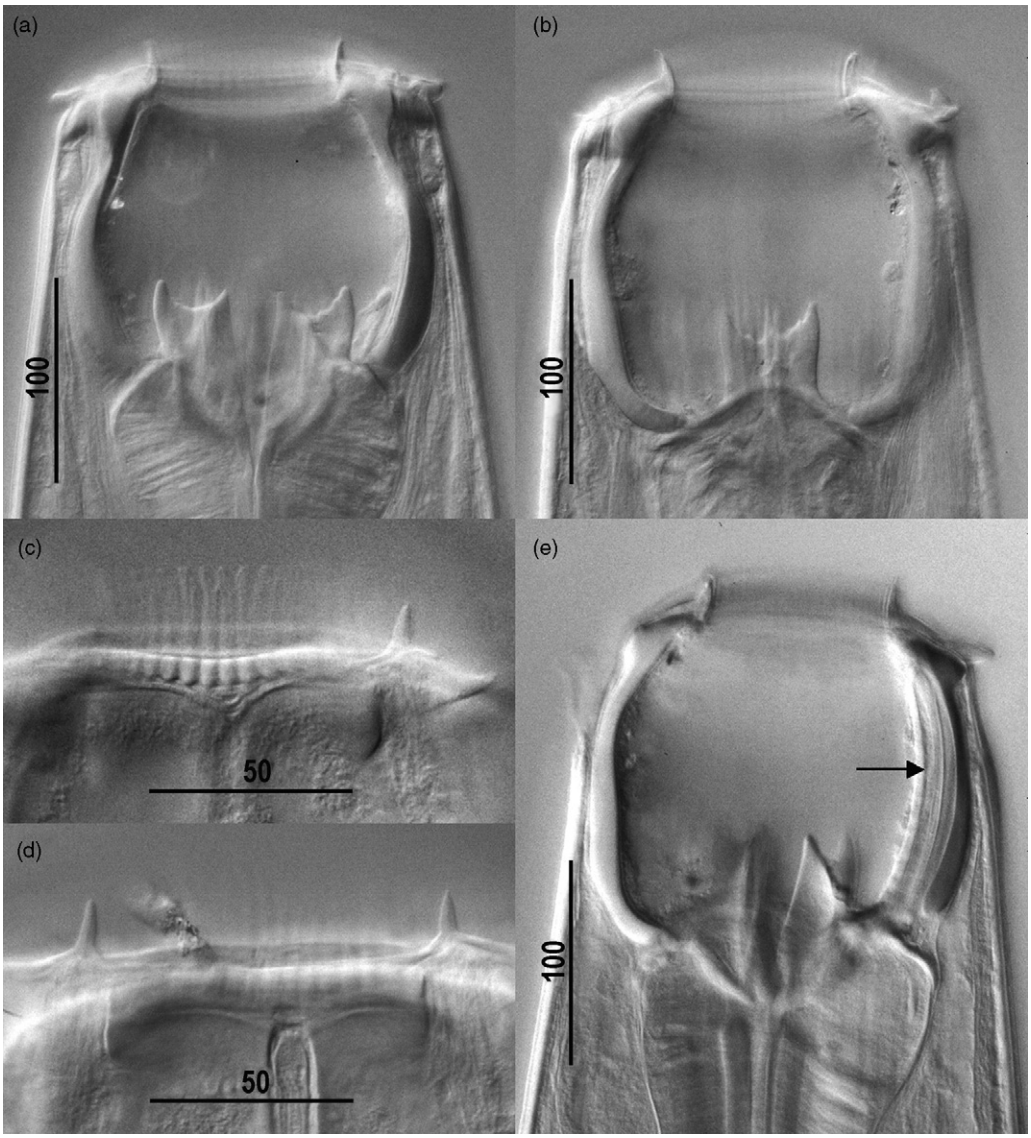

Fig. 18. *Triodontophorus burchelli*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, dorsal view, showing dorsal esophageal tooth. (c) Mouth collar, dorsal view, showing submedian papilla and elements of ELC and ILC. (d) Submedian papillae and dorsal gutter. (e) Buccal capsule, lateral view, showing dorsal gutter (arrow) and dorsal esophageal tooth.

650–824. Vulva to tail tip 592–812. Anus to tail tip 157–202. Egg size 66–102 × 33–57.

Hosts. *E. burchelli*.

Locality. Cecum, colon.

Distribution. Africa.

5.6.5. T. hartmannae Krecek et al., 1997 (Figs. 19 and 20)

General. Mouth collar flattened. Submedian papillae long, narrow, and pointed. ELC and ILC elements number 55–73. Buccal cavity oval, longer than wide. Upper edge of esophageal teeth with many small denticulations. Cuticle striated but relatively smooth.

Male. Body length 12.6–17.3 mm. Esophagus length 0.7–1.2 mm. BC width 135–183, depth 180–204. Anterior end to: deirids 777–870; excretory pore 812–940. Spicule length 0.9–1.1 mm. Gubernaculum length 224–280. Dorsal ray length 441–580. Dermal collar poorly developed on ventral side of genital cone. Two pairs of finger-shaped, branched appendages on genital cone.

Female. Body length 12.5–16.8 mm. Esophagus length 1.0–1.2 mm. BC width 135–177, depth 165–

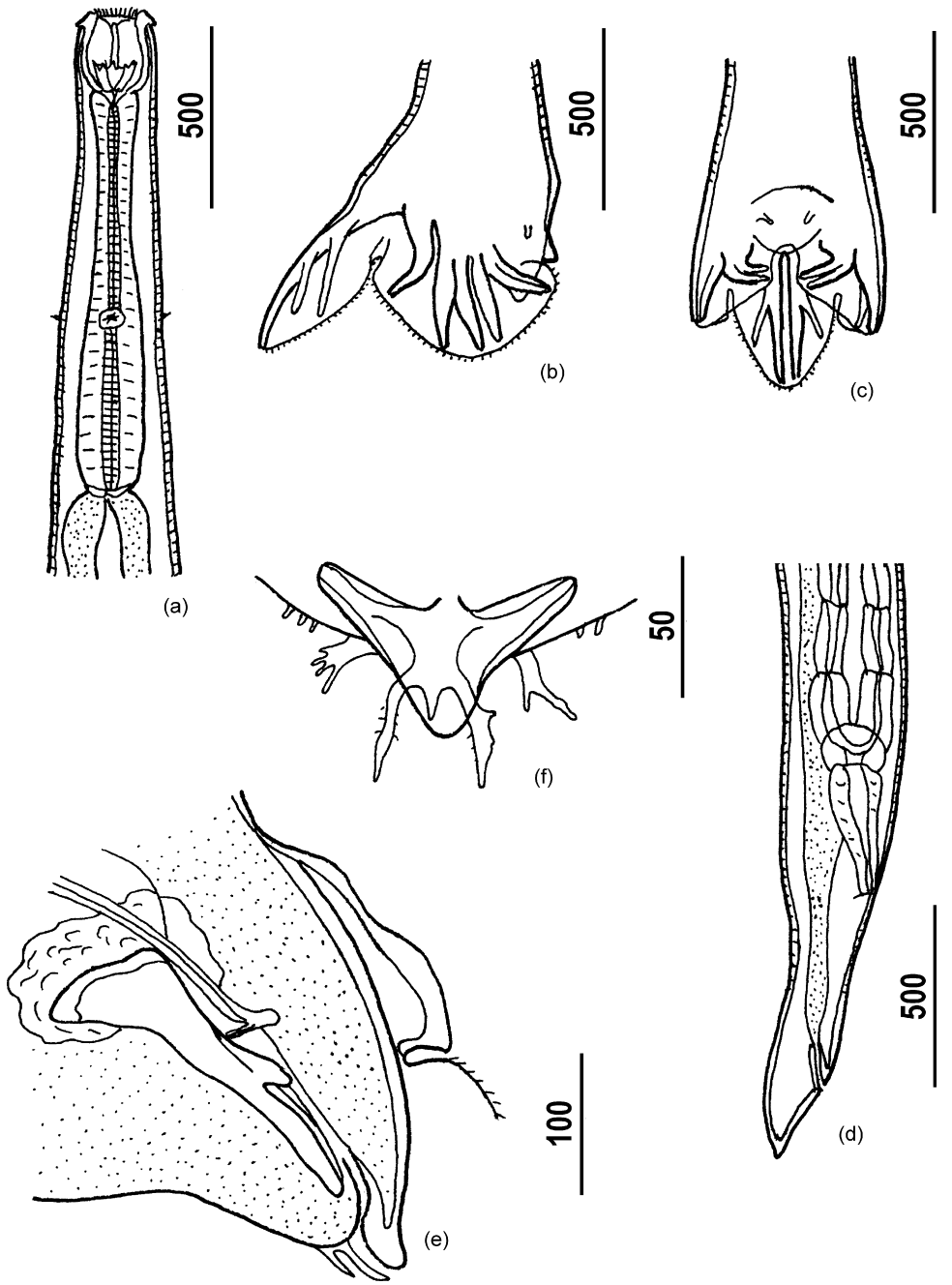

Fig. 19. *Triodontophorus hartmannae*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view.(f) Tip of genital cone, ventral view. (e modified from Krecek et al., 1997).

204. Anterior end to: deirids 556–893; excretory pore 568–940. Vulva to tail tip 661–916. Anus to tail tip 157–252. Egg size 75–93 × 39–48.

Hosts. *E. zebra hartmannae*.

Locality. Cecum, colon.

Distribution. Africa.

5.6.6. T. minor (Looss, 1900) Looss, 1902 (Figs. 21 and 22)

Synonyms. *Triodontus minor* Looss, 1900.

General. Mouth collar flattened. Submedian papillae short, conical. ELC and ILC elements number 44–49. Buccal cavity oval, slightly wider than deep or nearly

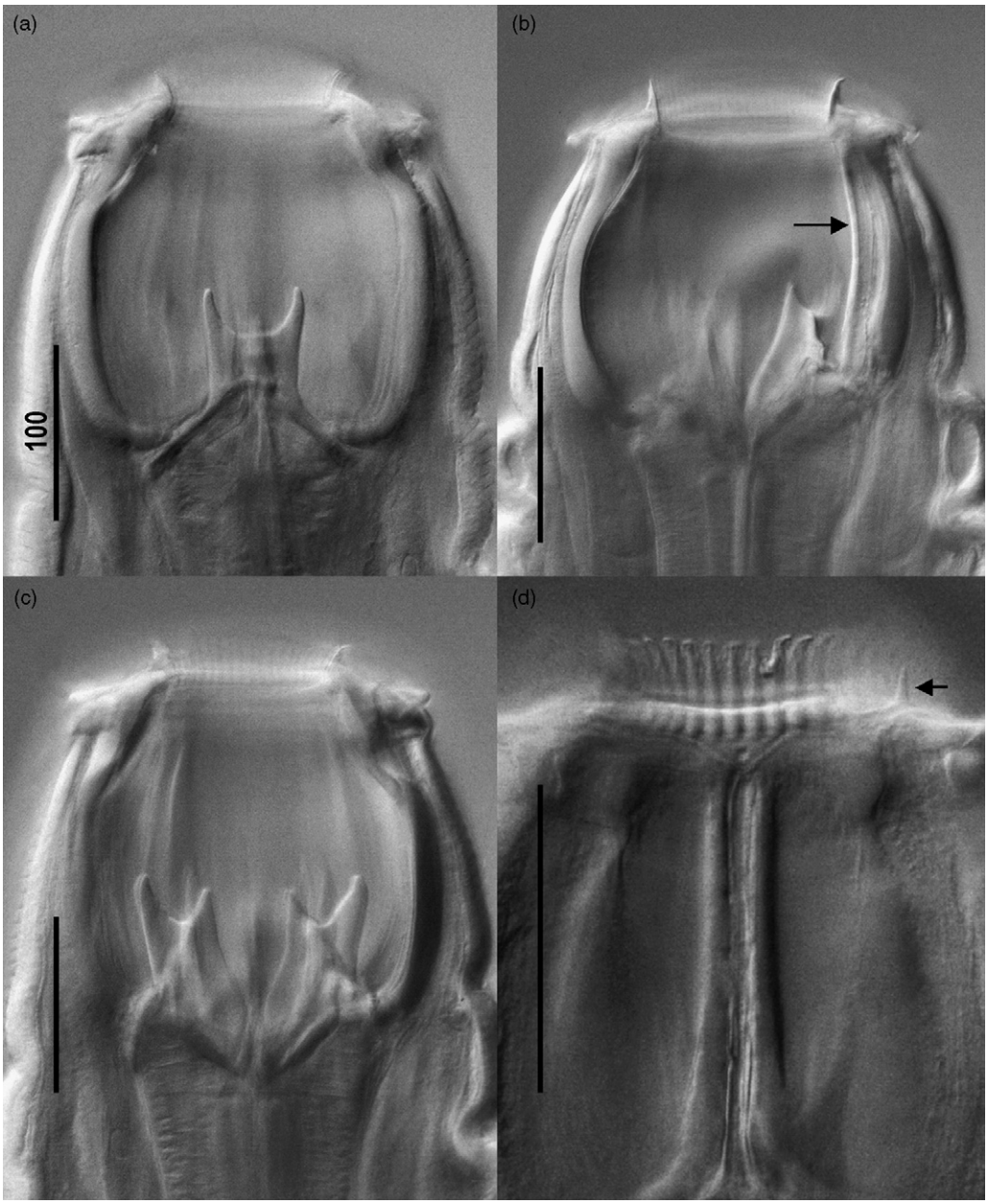

Fig. 20. *Triodontophorus hartmannae*. (a) Buccal capsule, dorsoventral view, showing dorsal esophageal tooth. (b) Buccal capsule, lateral view. Arrow marks dorsal gutter. (c) Buccal capsule, ventral view, showing two subventral esophageal teeth. (d) Submedian papilla (arrow), elements of ELC and ILC and dorsal gutter.

round. Upper edge of esophageal teeth with many small to medium denticulations. Cuticle striated but relatively smooth.

Male. Body length 8.5–13.4 mm. Esophagus length 0.89–1.10 mm. BC width 144–162, depth 135–159. Anterior end to: deirids 515–858; excretory pore 543–917. Spicule length 1.2–1.4 mm. Gubernaculum length 259–273. Dorsal ray length 578–593. Dermal collar well-developed on ventral side of genital cone. Genital cone with two branched appendages surrounded by tiny setae.

Female. Body length 10.1–16.0 mm. Esophagus length 0.89–1.20 mm. BC width 159–180, depth 159–180. Anterior end to: deirids 729–930; excretory pore 729–944; NR 501–572. Vulva to tail tip 543–862. Anus to tail tip 95–157. Egg size 86–99 × 43–54.

Hosts. *E. asinus*, *E. hemionus*.

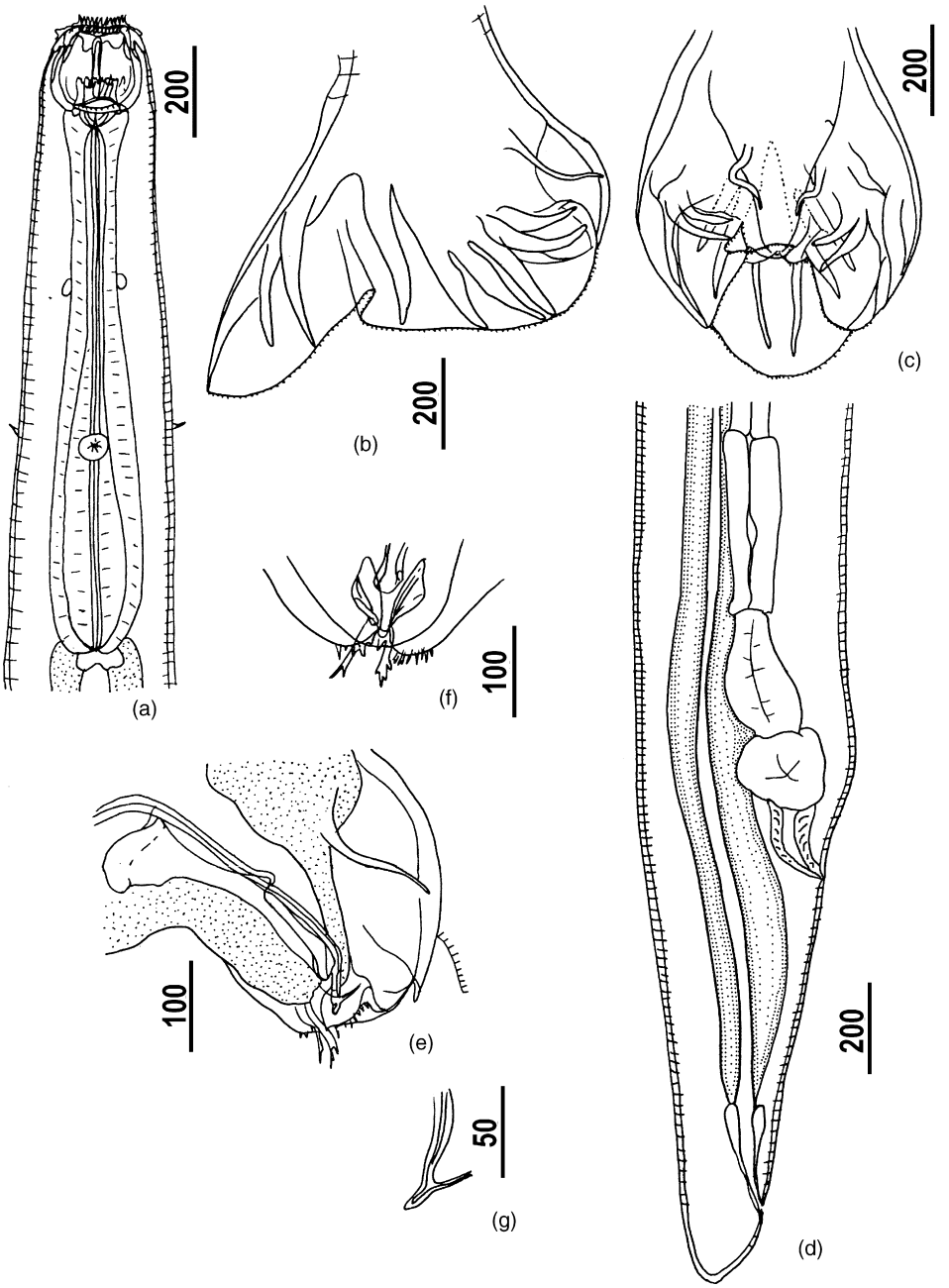

Fig. 21. *Triodontophorus minor*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

Locality. Cecum, colon.

Distribution. Europe, Asia, Africa.

5.6.7. T. nipponicus Yamaguti, 1943 (Figs. 23 and 24)

Synonyms. *Triodontophorus bronchotribulatus* Martines Gomez, 1966; *Triodontophorus hsiungi* K'ung, 1958.

General. Mouth collar flattened. Submedian papillae short, conical. ELC and ILC elements number 58–72. Buccal cavity almost round, nearly as wide as deep. Upper edges of esophageal teeth deeply denticulated. Cuticle striated but relatively smooth.

Male. Body length 8.1–16.8 mm. Esophagus length 0.8–1.2 mm. BC width 156–228, depth 130–180. Spicule length 0.85–1.12 mm. Gubernaculum length

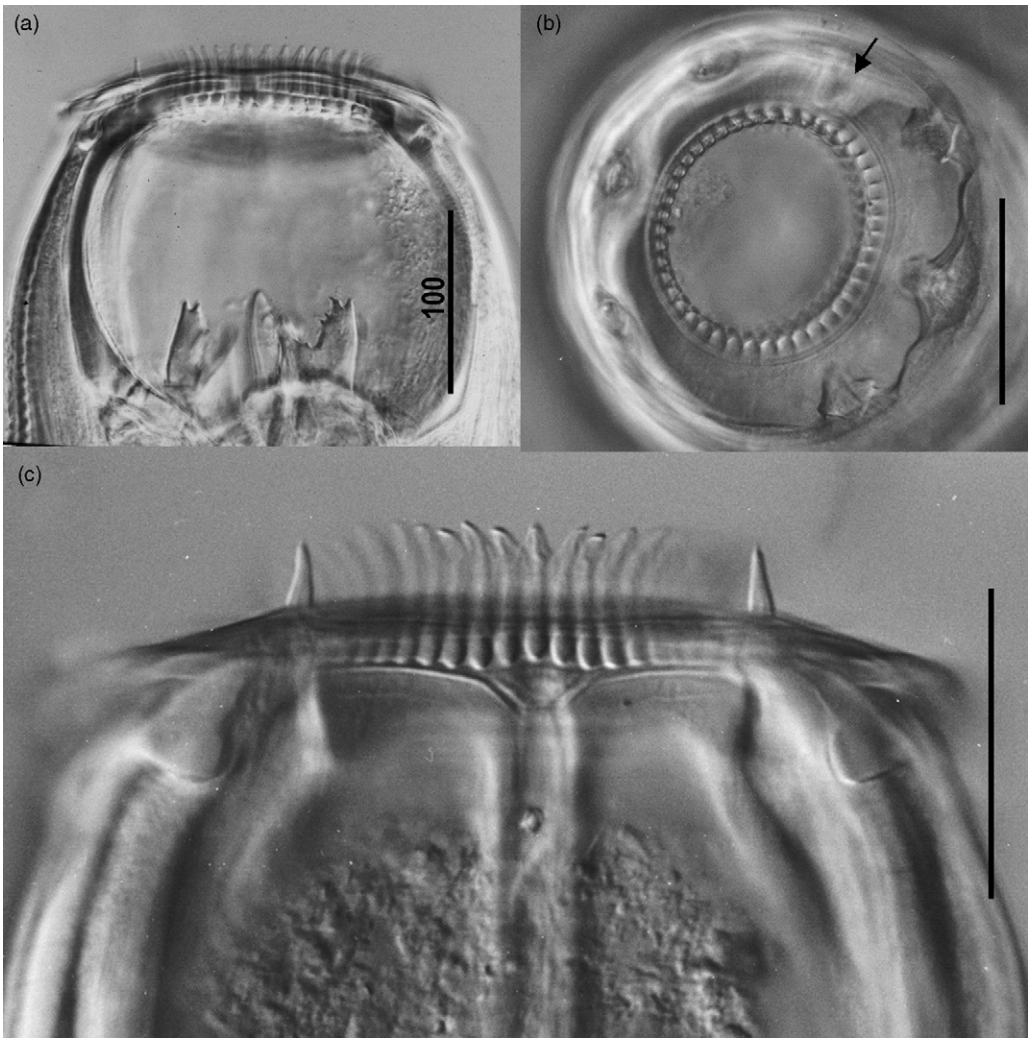

Fig. 22. *Triodontophorus minor*. (a) Buccal capsule, dorsoventral view. (b) Optical section at level of ILC. Arrow marks dorsal gutter. (c) Mouth collar, dorsal view, showing submedian papillae, elements of ELC and ILC and dorsal gutter (from Lichtenfels, 1975).

263–272. Dorsal ray length 565–603. Dermal collar poorly developed on ventral side of genital cone. Appendages of genital cone inconspicuous.

Female. Body length 11–18.5 mm. Esophagus length 0.9–1.5 mm. BC width 156–228, depth 130–180. Anterior end to: deirids 650–750; excretory pore 660–710. Vulva to tail tip 570–984. Anus to tail tip 120–230. Egg size 90–99 × 48–52.

Hosts. *Equus caballus*, *E. przewalskii*, *E. hemionus*.

Locality. Cecum, colon.

Distribution. Asia, Europe, North America, South America.

5.6.8. *T. tenuicollis* Boulenger, 1916 (Figs. 25 and 26)

Synonyms. *Triodontophorus popovi* Ershov, 1931.

General. Mouth collar flattened. Submedian papillae short, conical. ELC and ILC elements number 50–52. Buccal cavity oval, wider than long. Upper edge of esophageal teeth with many small to medium denticulations. Cuticle strongly serrated in cervical region.

Male. Body length 19.0–20.0 mm. Esophagus length 972–978. BC width 129, depth 111–116. Spicule length 1.13–1.14. Gubernaculum length 252–264. Dorsal ray length 231–248. Dermal collar poorly developed on ventral side of genital cone. Appendages of genital cone undeveloped.

Female. Body length 19.5–20.1 mm. Esophagus length 0.97–1.15 mm. BC width 129–136, depth 109–115. Anterior end to deirids 891. Vulva to tail tip 586–599. Anus to tail tip 129–136. Egg size 84–98 × 41–49.

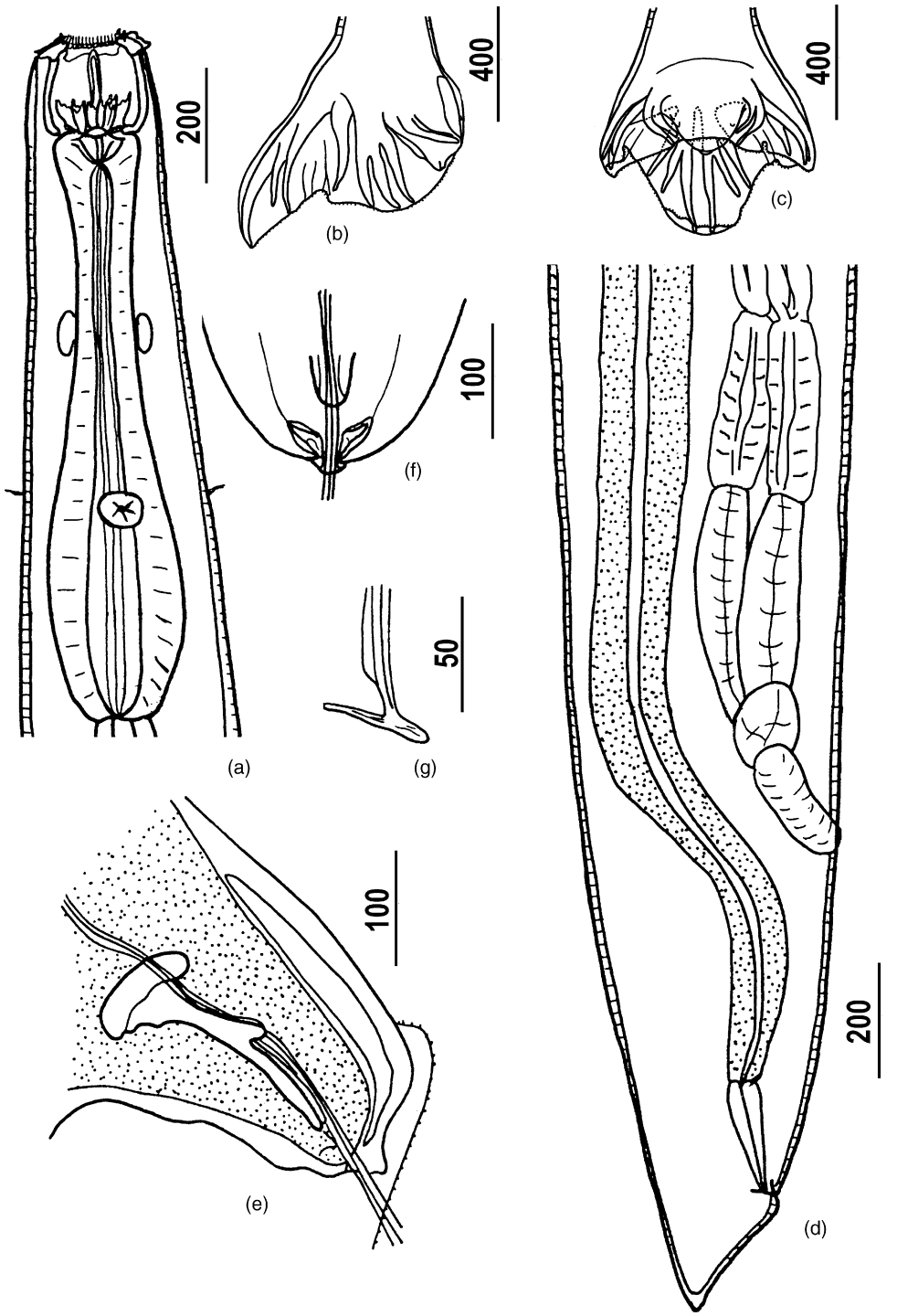

Fig. 23. *Triodontophorus nipponicus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

5.6.9. Discussion

Initially this genus included two species, *T. minor* and *T. serratus*, differentiated by their size, copulatory organs structure, mouth collar height and the shape of

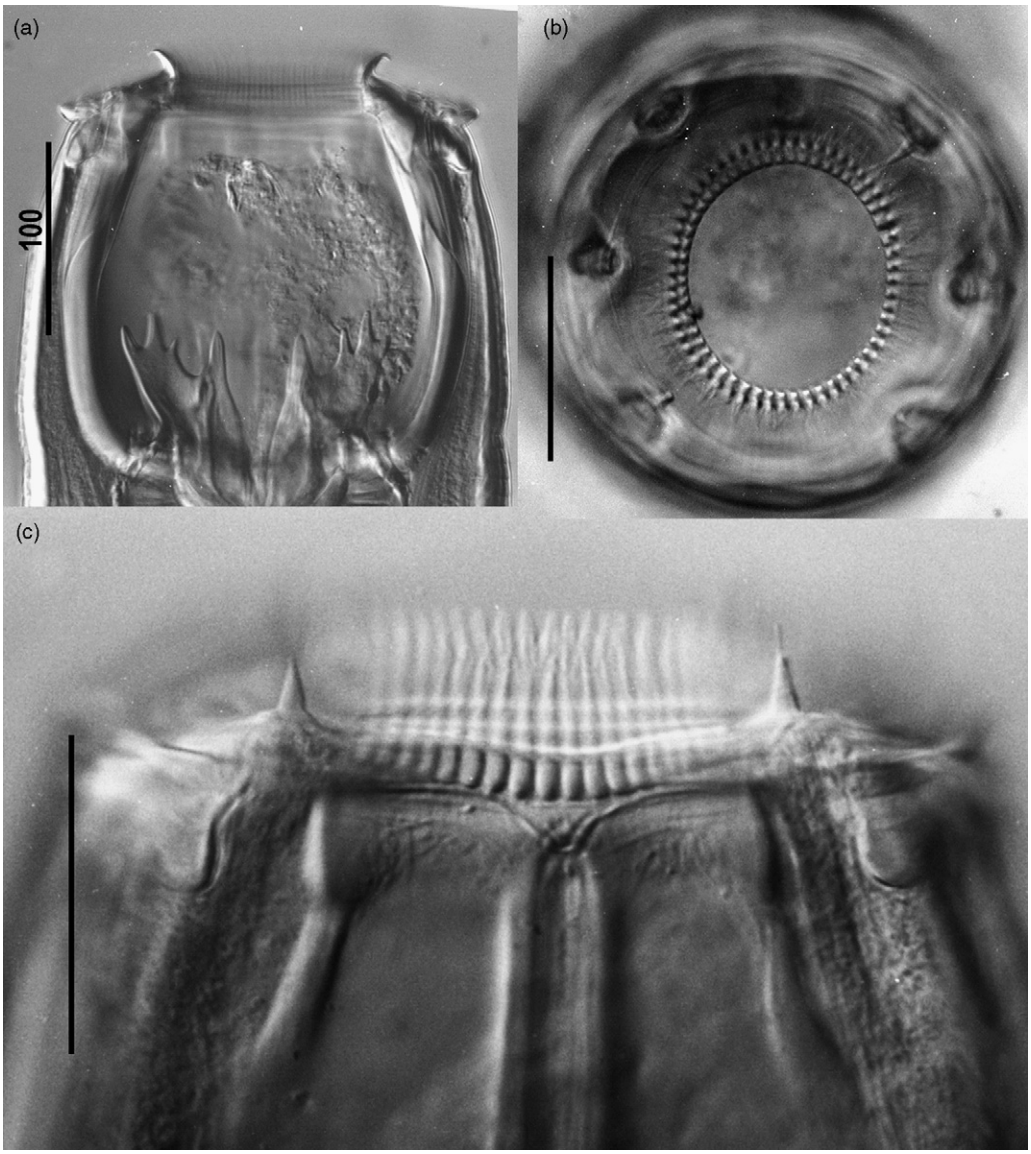

Fig. 24. *Triodontophorus nipponicus*. (a) Buccal capsule, dorsoventral view, showing subventral esophageal teeth. (b) Optical section at level of ILC. (c) Mouth collar, dorsal view, showing submedian papillae, elements of ELC and ILC and dorsal gutter (from Lichtenfels, 1975).

the denticulations of esophageal teeth which in *T. minor* are ''generally smooth'', and in *T. serratus* ''are more or less strongly serrated'' (Looss, 1902).

In 1909, on the basis of an examination of some females from Australia, Sweet (1909) described *T. intermedius* which was close to *T. serratus* and differed from it mainly morphometrically.

Based on material from horses of Great Britain, the description of *T. intermedius* was expanded by Boulenger (1916), and two new species were described—*T. brevicauda* and *T. tenuicollis*. The first was clearly distinguished by its large buccal capsule and some other peculiarities, and the second by a slender anterior end and strongly serrated cuticle. Theiler, 1924, while studying specimens of *Triodontophorus* from horses and donkeys from South Africa, redescribed *T. serratus*, *T. brevicauda* and *T. tenuicollis*, and determined that *T. intermedius* is synonymous with *T. serratus*.

In Boulenger (1921), when studying specimens from horses in India, extended the description of *T. minor* and noted that denticulation of esophageal teeth is greatly varied among species. Among *T. serratus* the author found specimens with smooth dental plates and concluded that the shape of the upper edge of dental

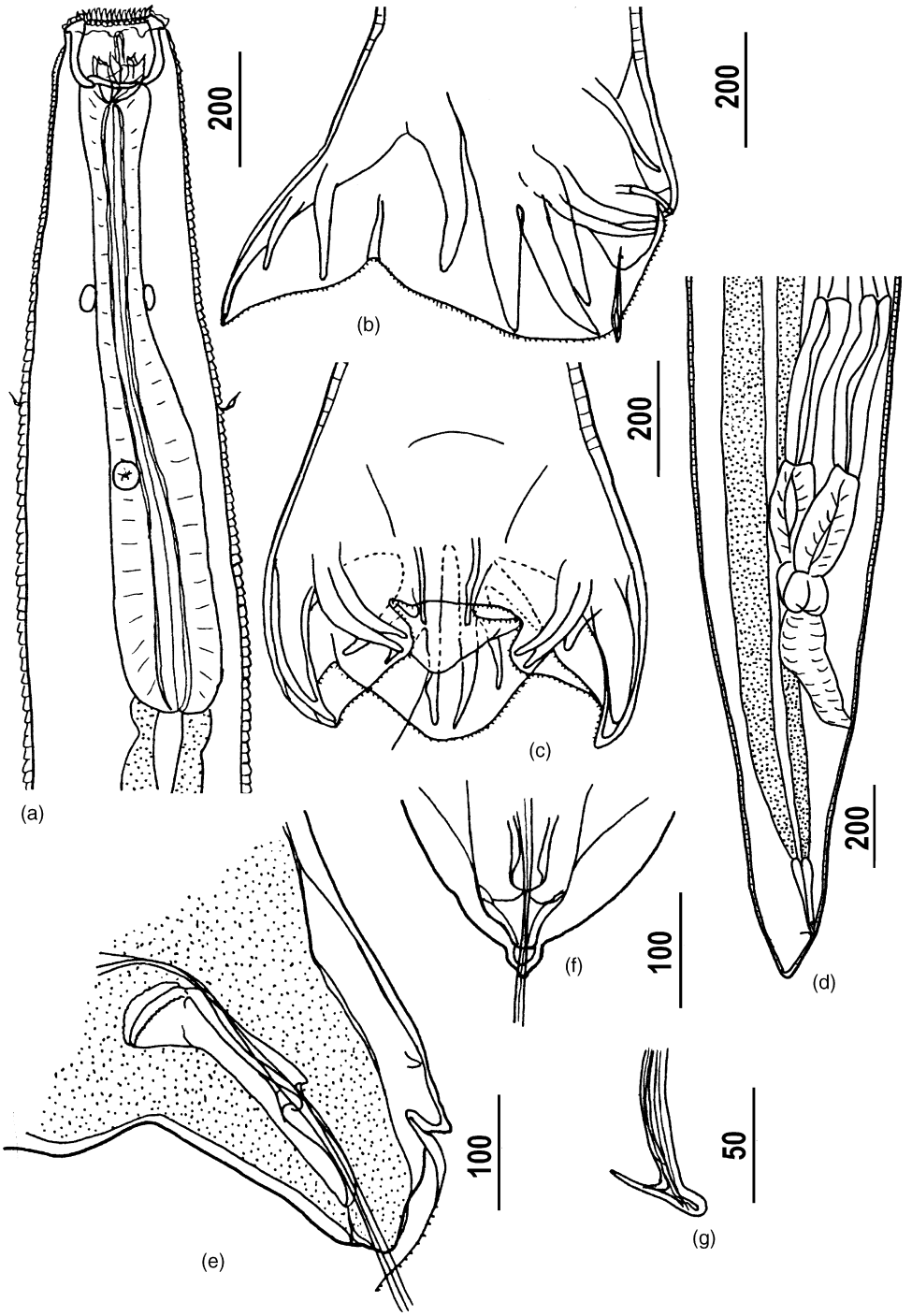

Fig. 25. *Triodontophorus tenuicollis*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (from Dvojnos and Kharchenko, 1994).

plates could not be a reliable diagnostic feature. However, this character was considered by Lichtenfels (1975) to be useful for identifying species and Dvojnos and Kharchenko (1985) concluded that although tooth serration varies within species differences among species are greater and are useful for identifying species of *Triodontophorus*.

In 1931 Ershov described *T. popovi* from Siberian horses and differentiated it from *T. tenuicollis* morphometrically and by teeth placement in the buccal

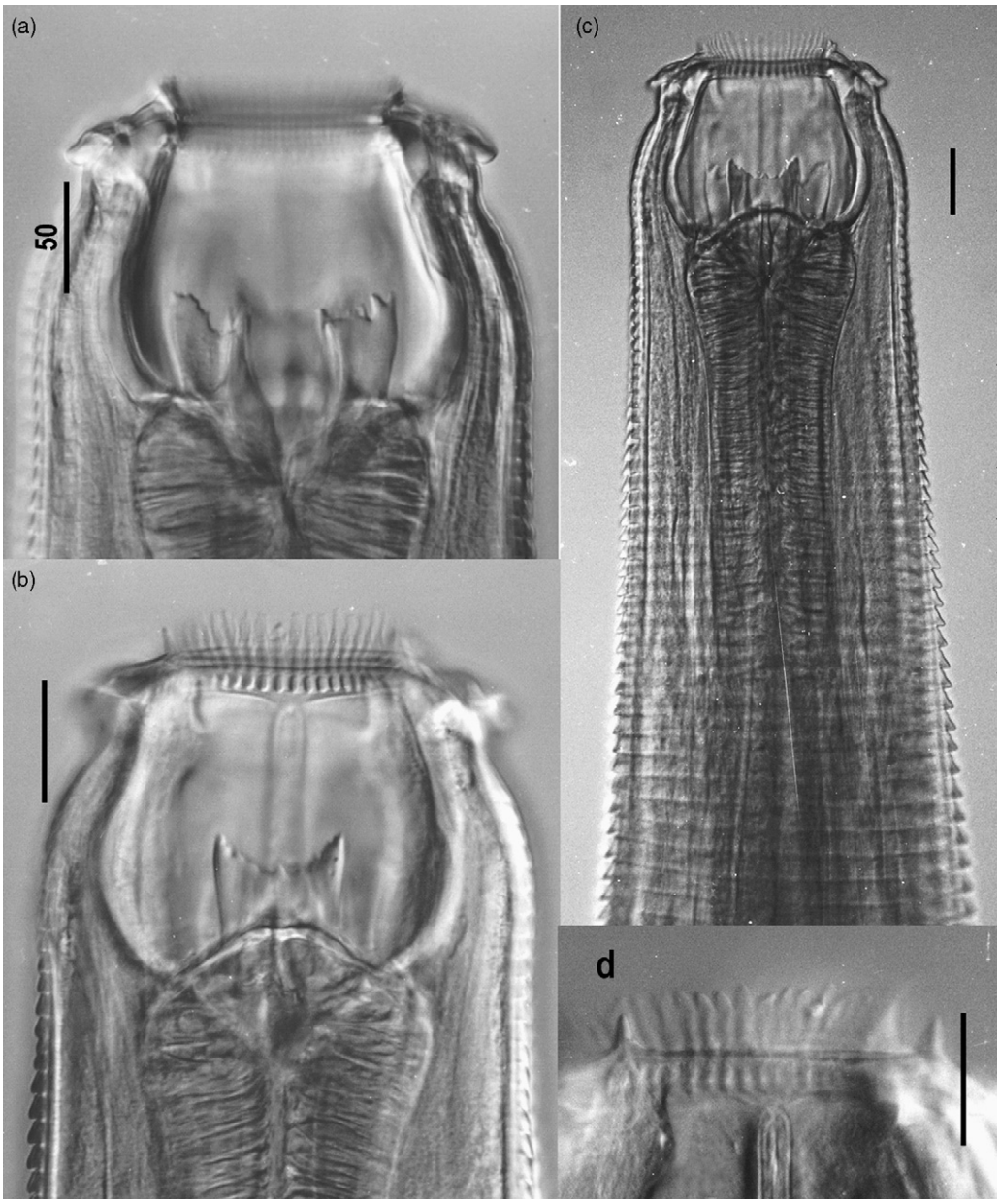

Fig. 26. *Triodontophorus tenuicollis*. (a) Buccal capsule, dorsoventral view, showing subventral teeth. (b) Buccal capsule, dorsal view, showing dorsal esophageal tooth. (c) Anterior end showing serrated cuticle. (d) Submedian papillae, elements of ELC and ILC and tip of dorsal gutter (modified from Lichtenfels, 1975).

capsule (Skrjabin and Ershov, 1933). *Triodontophorus popovi* was subsequently regarded by Dvojnos and Kharchenko (1985) to be a synonym of *T. tenuicollis*.

From Japanese and Korean horses, *T. nipponicus* was described (Yamaguti, 1943) which differed from *T. minor* by spicule length, and teeth shape, having three large projections on each on the teeth.

From donkeys from Peking *T. hsiungi* was described (K'ung, 1958) which is similar to *T. nipponicus*. K'ung et al. (1959) listed *T. hsiungi* as one of the most common strongyles in donkeys in Peking. In 1963 *T. hsiungi* was synonomized with *T. nipponicus by* Diaz-Ungria (1963).

In 1966, from Spanish horses, *T. bronchotribulatus* was described (Martines Gomez, 1966). This species was considered by Dvojnos and Kharchenko (1985) to be a synonym of *T. nipponicus*.

Lichtenfels, 1975 could confirm no reports of *T. minor* in North America but did reveal *T. nipponicus*

including some that had been previously identified as *T. minor*.

Krecek et al. (1997) described two species from zebras, *T. burchelli* and *T. hartmannae*. *Triodontophorus burchelli* bears a close resemblance to *T. brevicauda*. This species can be distinguished from *T. brevicauda* by a greater body length in the male, greater distances of the vulva to the tip of tail and anus to tip of tail. *Triodontophorus hartmannae* differs from *T. nipponicus* both in the longer distance from the vulva to the tip of the tail and less pointed serration of the teeth. *T. hartmannae* has shorter spicules than *T. minor*.

6. Cyathostominae

6.1. *Cyathostomum (Molin, 1861) Hartwich, 1986*

Synonyms. *Trichonema* Cobbold, 1874; *Cylicostomum* Looss in Railliet, 1901; *Cylichnostomum* Looss, 1902; *Cylicostoma* Looss, 1911; *Cylicocercus* Ihle, 1922; *Cylicostomias* Cram, 1925.

General. Medium-sized Cyathostominea. MC inflated, high, ring-shaped, divided into inner and outer rings. Posterior edge of MC situated at, anterior, or posterior to anterior edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae bullet-shaped, two to three times as long as thick. Stalk of submedian papillae longer than broad. ELC elements markedly less numerous and longer than those of ILC. Elements of ELC longer than broad, tip pointed; insertion point slightly back from tips of elements of ILC. Elements of ILC longer than broad, tips pointed; insertion point about 1/4−1/2 of BC depth. Line formed by insertion of elements of ILC curved or sinuous. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, elongate, curving, thin at one end. Septum intracoronare origin on support. Medial insertion of septum intracoronare anterior to junction of ELC and ILC. Walls of BC straight, thicker posteriorly, but without ring-like thickening. Buccal cavity cylindrical, wider than deep. Dorsal gutter nipple- or button-like. Buccal teeth absent. Esophageal funnel shallow. Esophageal teeth not prominent. Anterior muscular portion of esophagus about 1/4−1/3 of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches. Ventral rays shorter or of equal length to laterals (longer in *C. alveatus*). Dorsal lobe longer then lateral lobes. Externodorsal rays origin at junction of dorsal and laterals rays. Gubernaculum large, with dorsal handle and ventral notch. Genital cone short, conical. Spicule tips pick-shaped.

Female. Vulva about one, or less than one, tail length from anus. Vagina longer than ovejector sphincter. Ovejector vestibule oval or Y-shaped; infundibulum longer than sphincter. Tail digitiform, short, length less than 2× diameter at anus.

Type species. *C. tetracanthum* (Mehlis, 1831) Molin, 1861, in part; Looss, 1900

6.1.1. *Key to species of Cyathostomum*

(1) a. Junction of support (S) for ELC and wall of BC marked by narrow constriction	2
b. Junction of S and BC without narrow constriction	4
(2) a. S nearly as large as wall of BC	*C. tetracanthum*
b. S much smaller than wall of BC	3
(3) a. Elements of internal leaf-crown (ILC) inserted on medial wall of BC in sinuous line in lateral view	*C. pateratum*
b. ILC inserted in convex line laterally	*C. catinatum*
(4) a. S and wall of BC much shorter laterally than dorsally and ventrally; ILC inserted at 1/2 depth of BC	*C. montgomeryi*
b. S and wall of BC of similar height laterally, dorsally and ventrally; ILC inserted at 1/5 of depth of BC	*C. alveatum*

6.1.2. *C. tetracanthum (Mehlis, 1831) Molin, 1861, in part, Looss, 1900 (Figs. 27 and 28)*

Synonyms. *Strongylus tetracanthus* Mehlis, 1831, in part; *Sclerostomum tetracanthum* (Mehlis, 1831) Diesing, 1851, in part; *Cylichnostomum tetracanthum* (Mehlis, 1831) Looss, 1902; *Cylicostomum tetracanthum* (Mehlis, 1831) Gedoelst, 1903; *Cylicostoma tetracanthum* (Mehlis, 1831) Looss, 1911; *Trichonema tetracanthum* (Mehlis, 1831) Railliet, 1919; *Trichonema arcuata* Cobbold, 1874, in part; *Trichonema aegyptiacum* Railliet, 1923; *Cylicostomum aegyptiacum* (Railliet, 1923) Cram, 1924; *Cylicostomias aegyptiaca* (Railliet, 1923) Cram, 1925; *Erschowinema aegyptiacum* (Railliet, 1923) Tschoijo, 1957; *Sclerostoma quadridentatum* Dujardin, 1845, in part; not *Cyathostomum tetracanthum* sensu Hartwich, 1986; *Coronocyclus aegyptiacus* (Looss, 1900) Dvojnos and Kharchenko, 1990.

General. ELC with about 22 elements; ILC with about 66. Line formed by insertion of elements of ILC slightly more anterior dorsally and ventrally than

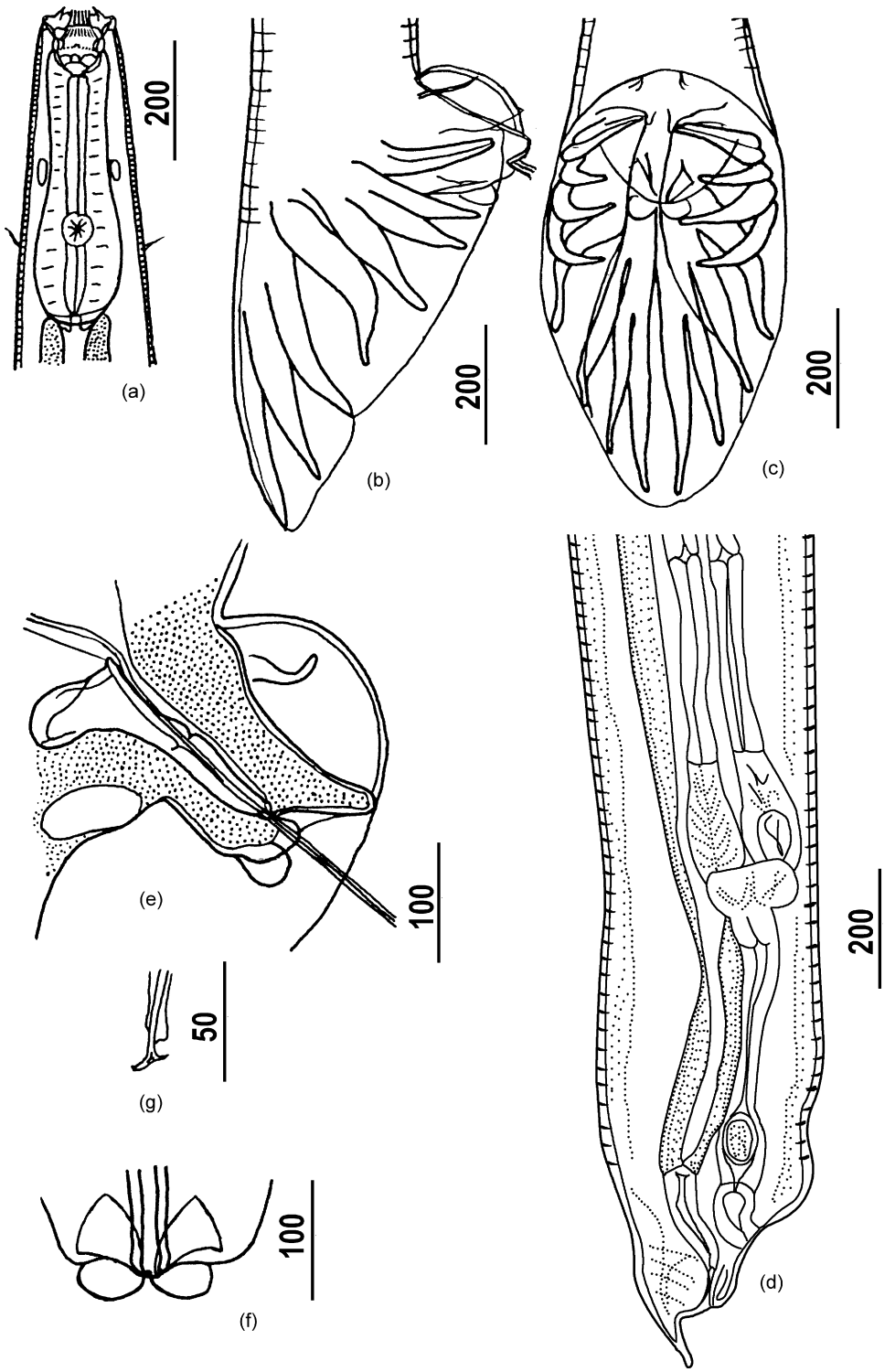

Fig. 27. *Cyathostomum tetracanthum*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (from Dvojnos and Kharchenko, 1994).

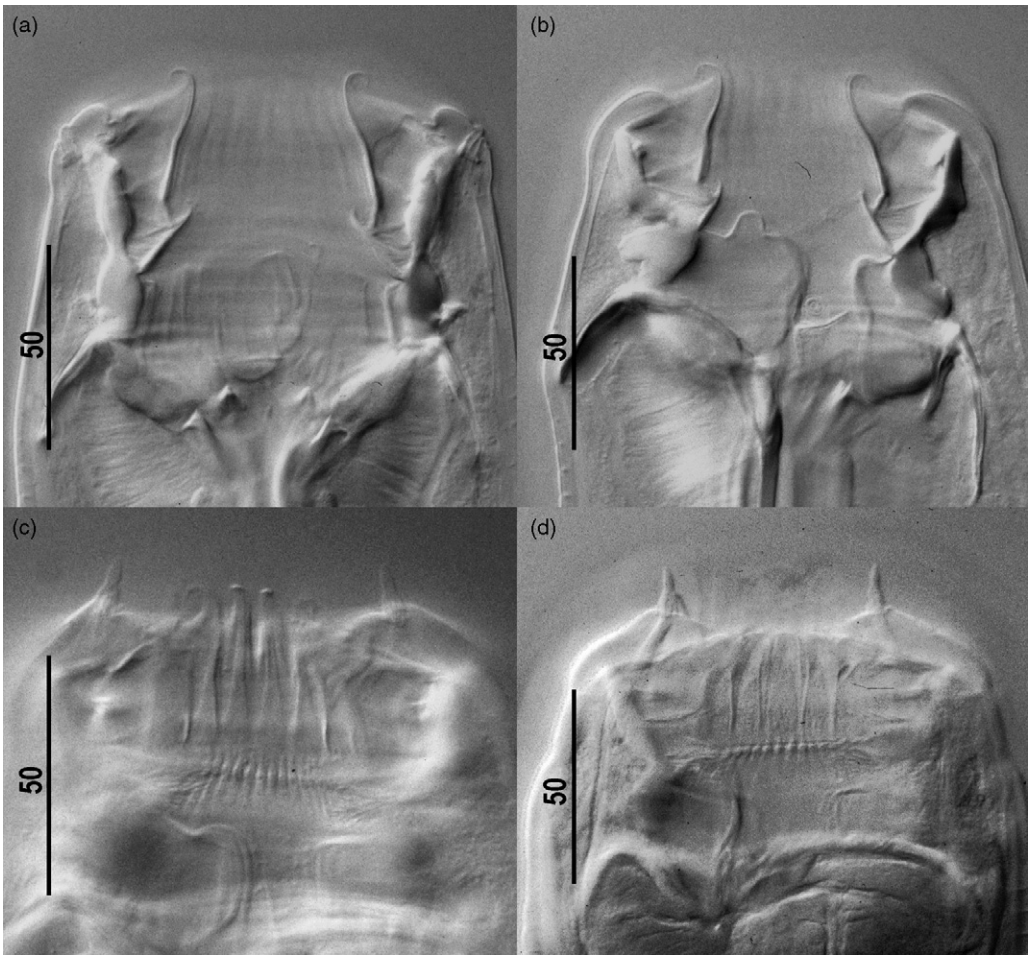

Fig. 28. *Cyathostomum tetracanthum*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing inflated cuticular lining of BC. (c) Elements of ILC and ELC. (d) Submedian papillae.

laterally. Support for ELC continuous with BC, but junction marked by constriction, elongate, curving, thin at anterior end. Support nearly as long as wall of BC. Deirids and excretory pore near middle of glandular esophagus, 280 from anterior end.

Male. Body length 7.0–9.0 mm. Esophagus length about 400. BC width 60, depth 12. Deirids to head end 280. Spicule length 1.8–2.1 mm. Gubernaculum length 198–208. Dorsal ray length 496–544. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone ovoid, with short blunt point arising on its posterior surface. Protrusions of dermal collar absent.

Female. Body length 8.0–12.0 mm. Esophagus length about 400. BC width 60, depth 12. Deirids to head end 280. Vulva to anus 140–200. Anus to tail tip 100–120. Egg size 76–80 × 36–40. Sublateral protrusions near vulva poorly developed.

Hosts. *Equus caballus*, *E. asinus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.1.3. *C. alveatum (Looss, 1900) Cram, 1924 (Figs. 29 and 30)*

Synonyms. *Cylichnostomum alveatum* (Looss, 1900) Looss, 1902; *Cylicostomum alveatum* (Looss, 1900) Gedoelst, 1903; *Cylicocercus alveatus* (Looss, 1900) Cram, 1924; *Trichonema alveatum* (Looss, 1900) Yorke and Maplestone, 1926; *Erschowinema alveatum* (Looss, 1900) Tschoijo, 1957.

General. ELC consists of about 29 elements; ILC about 90. Tips of elements of ILC pointed. Insertion point for posterior ends of elements of ILC about 1/5 of BC depth. ILC inserted in convex line in lateral view. Support for ELC continuous with BC. Junction of S and wall of buccal BC without narrow constriction. S much smaller than wall of BC. S and wall of BC of similar

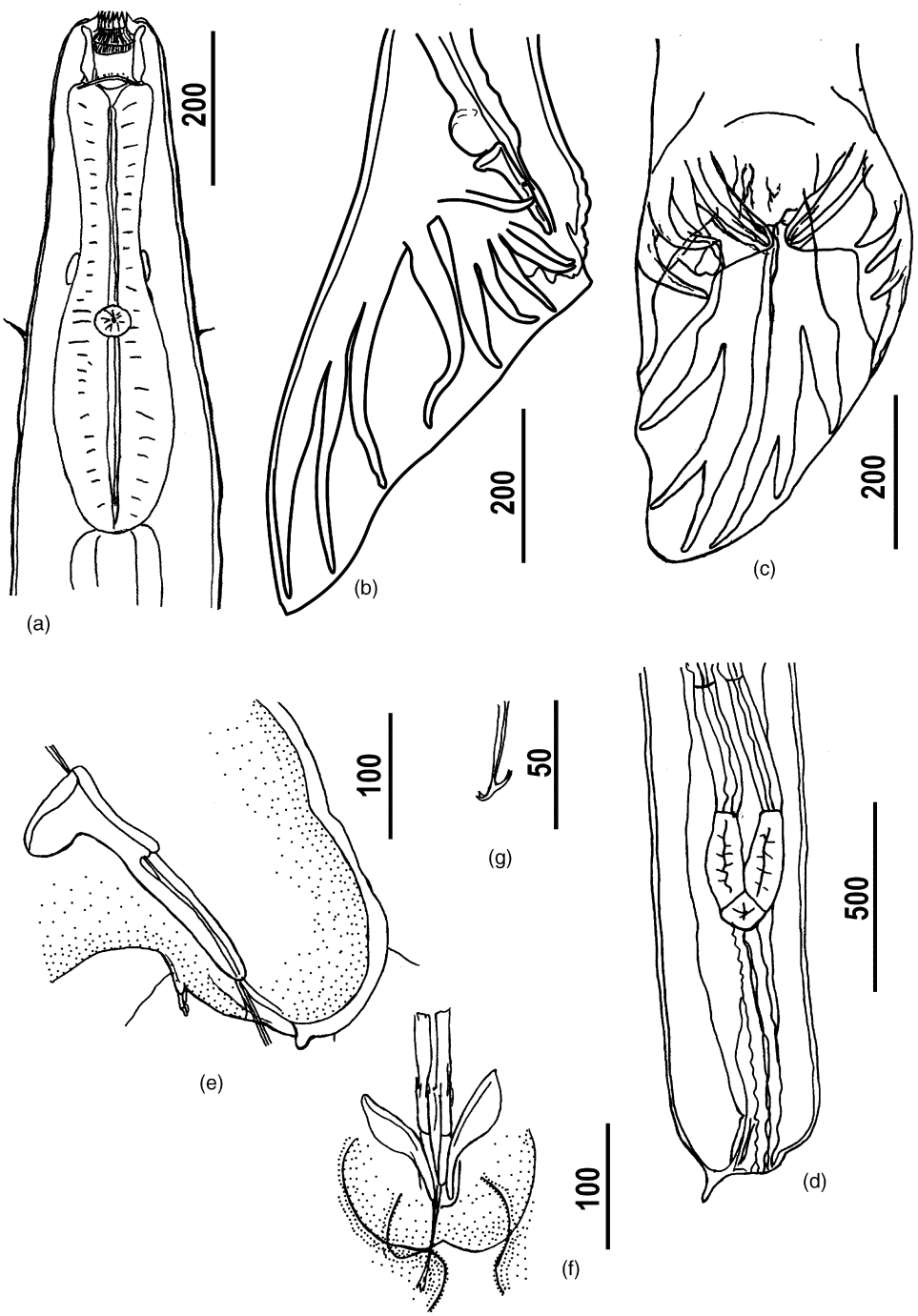

Fig. 29. *Cyathostomum alveatum*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (a, c–g from Dvojnos and Kharchenko, 1994).

height laterally, dorsally and ventrally. Excretory pore and deirids near middle of glandular esophagus, 360–390 from anterior end.

Male. Body length 10.0–10.5 mm. Esophagus length 660–800, width 150. BC width 48–54, depth 48–54. Spicule length 1.75–2.39 mm. Gubernaculum length 248–262. Dorsal ray length 560–620. Ventral rays longer than laterals. Appendages of genital cone cylindrical, slightly asymmetric; their distal ends elongated into rods with rounded ends. Protrusions of dermal collar absent.

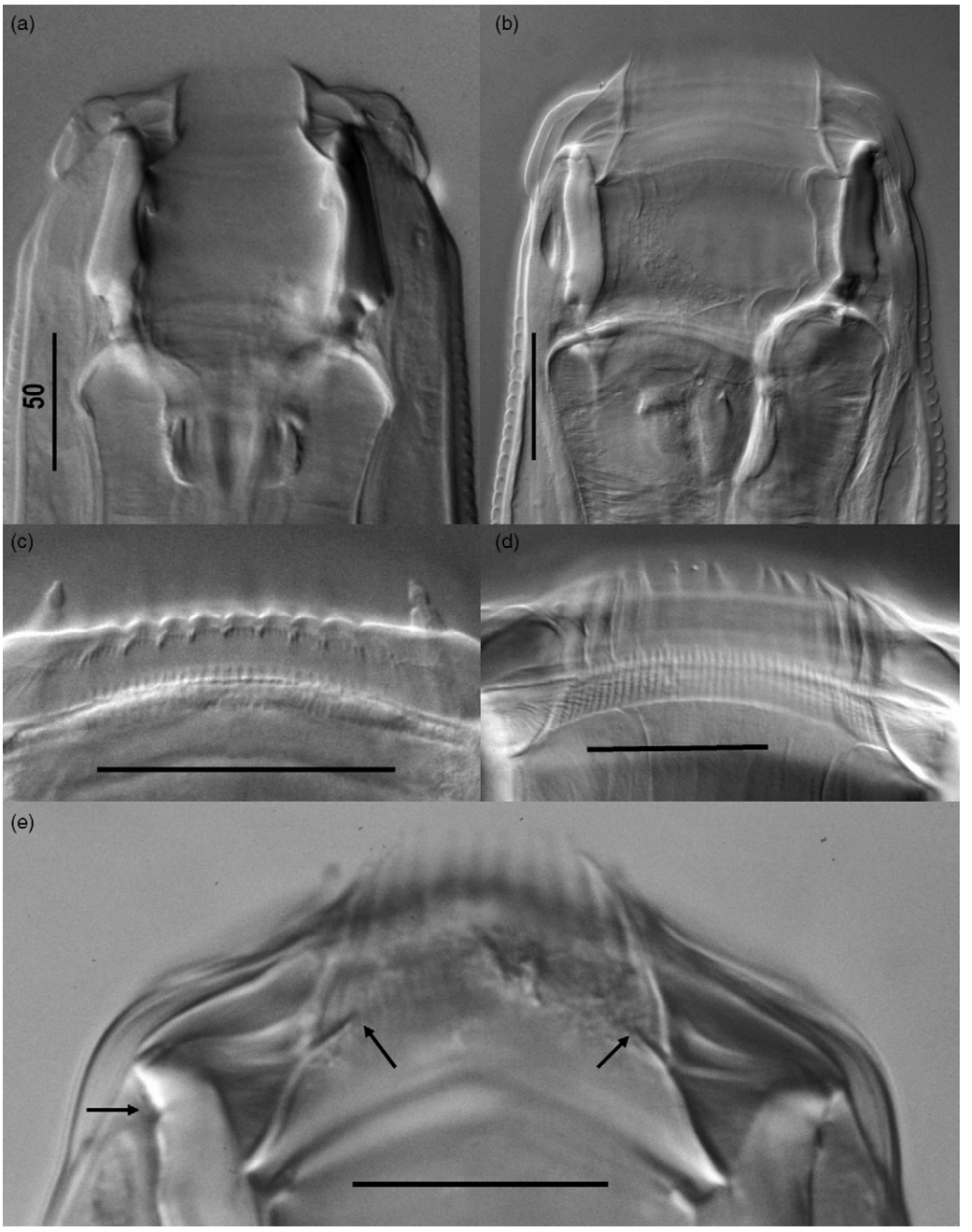

Fig. 30. *Cyathostomum alveatum*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Submedian papillae, elements of ILC. (d) Elements of ILC and ELC. (e) Elements of ILC (arrows at anterior tips) and support (arrow at junction of support and BC).

Female. Body length 10.5–13 mm. Esophagus length 660–800. BC width 68–100, depth 54–70. Vulva to anus 70–80. Anus to tail tip 70–80. Egg size 80–90 × 40–49.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.1.4. *C. catinatum* Looss, 1900 (Figs. 31 and 32)

Synonyms. *Cylichnostomum catinatum* (Looss, 1900) Looss, 1902; *Cylicostomum catinatum* (Looss, 1900)

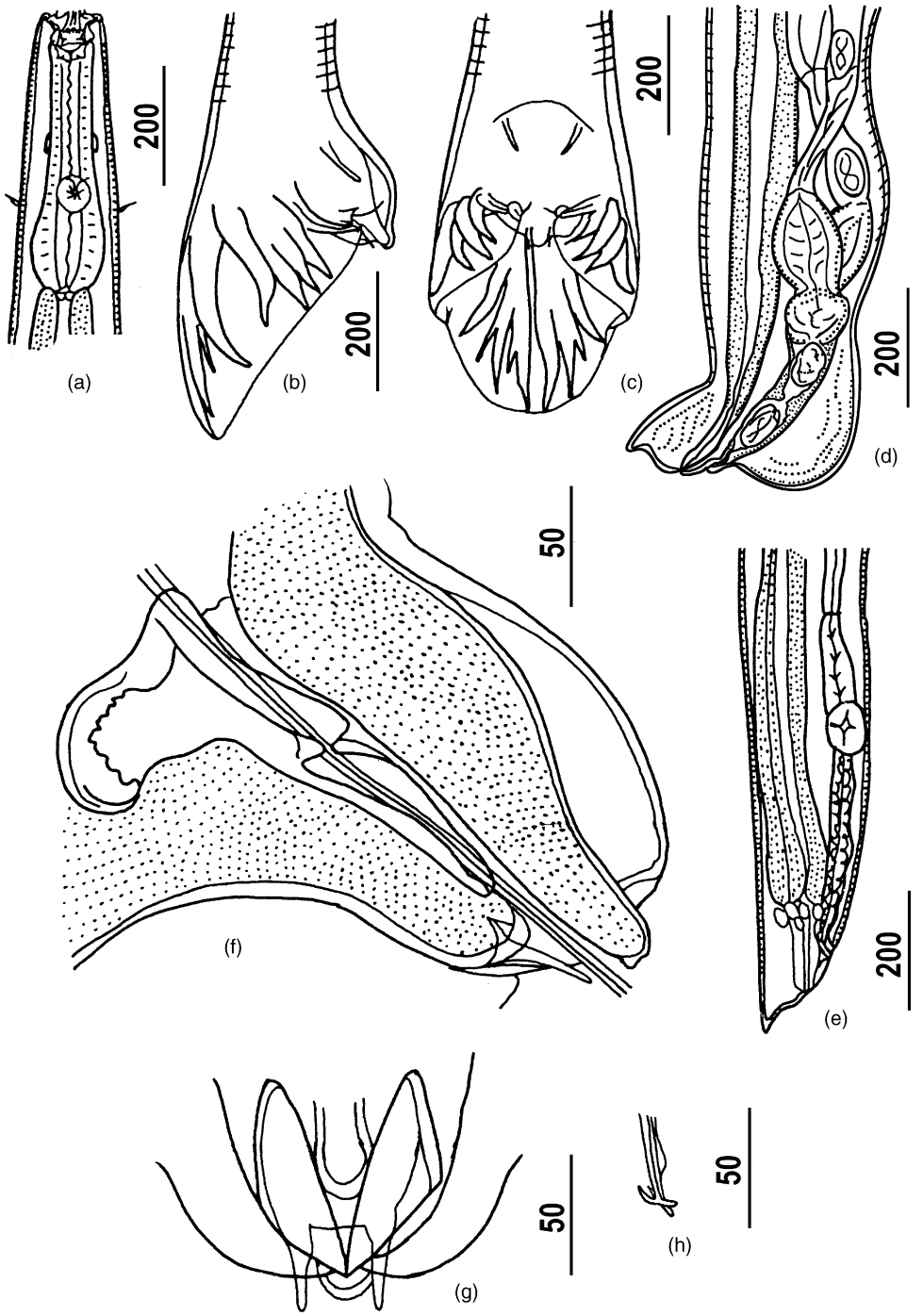

Fig. 31. *Cyathostomum catinatum*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) and (e) Tails of females, showing variations that may be due to maturity of specimen. (f) Genital cone, lateral view. (g) Tip of genital cone, ventral view. (h) Fused spicule tips of male (from Dvojnos and Kharchenko, 1994).

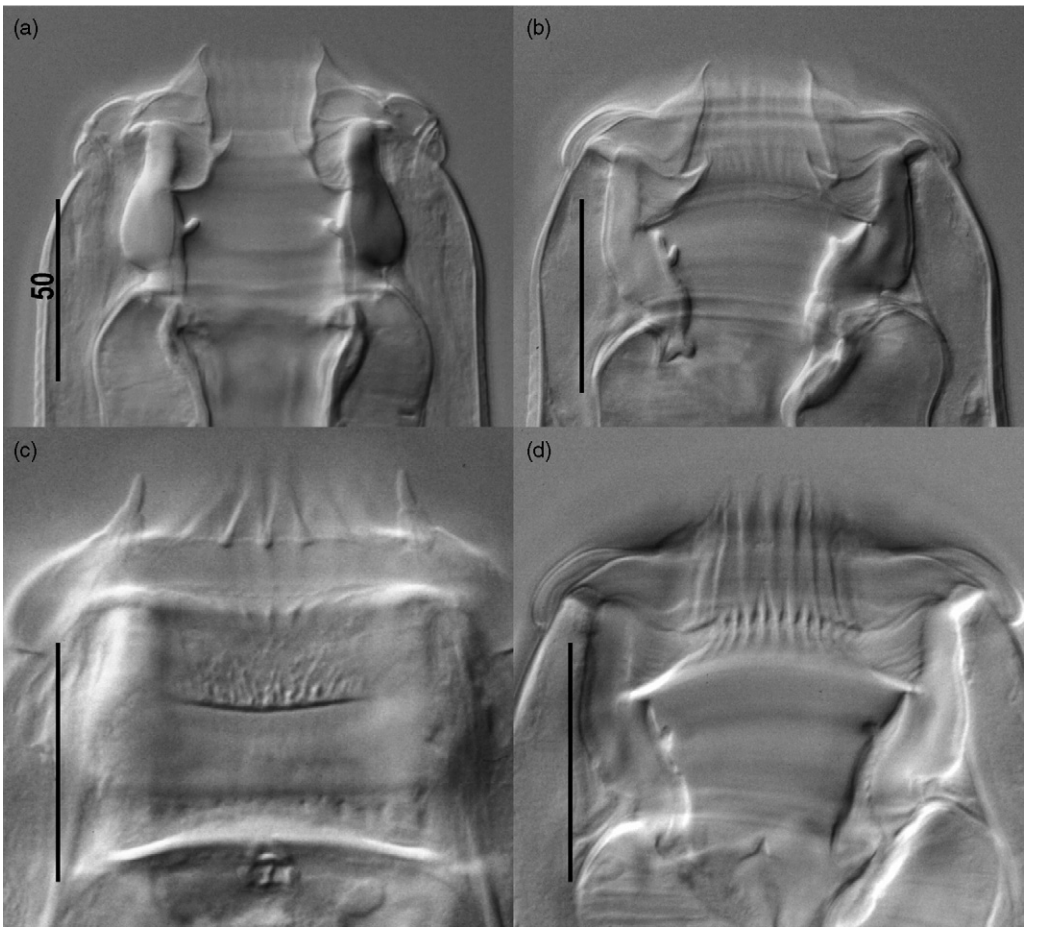

Fig. 32. *Cyathostomum catinatum*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Submedian papillae, elements of ILC and tiny dorsal gutter. (d) Elements of ELC and ILC and esophageal tooth, lateral view.

Gedoelst, 1903; *Trichonema catinatum* (Looss, 1900) Le Roux, 1924; *Cylicocercus catinatum* (Looss, 1900) Cram, 1924; *Erschowinema catinatum* (Looss, 1900) Tschoijo, 1957; *Cylicostomum pseudocatinatum* Yorke and Macfie, 1919; *Cylicostomum catinatum litoraureum* Yorke and Macfie, 1920; *Cylicostomum catinatum lopezneyrai* Lizcano Herrera, 1951.

General. ELC with 18–22 elements; ILC 30–40. ILC inserted in convex line in lateral view. Junction of support (S) for ELC and wall of BC marked by narrow constriction. S much smaller than wall of BC. Deirids near middle of glandular esophagus, 210–229 from anterior end.

Male. Body length 4.0–8.6 mm. Esophagus length 310–360. BC width 40–58, depth 19–26. Spicule length 1.12–1.52 mm. Gubernaculum length 180–208. Dorsal ray length (from distal tip to origin of externodorsal ray) 315–377. Ventral rays length equal to laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone inconsistent; studied specimens have two fingerlike projections. Protrusions of dermal collar absent.

Female. Body length 4.89–9.8 mm. Esophagus length 380–451. BC width 40–68, depth 20–29. Vulva to tail tip 98–195. Anus to tail tip 75–110. Egg size 95–105 × 44–48.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.1.5. C. montgomeryi (Boulenger, 1920) K'ung, 1964 (Figs. 33 and 34)

Synonyms. *Cylicostomum montgomeryi* Boulenger, 1920; *Cylicostomum montgomeryi* Boulenger, 1920; *Cylicotoichus montgomeryi* (Boulenger, 1920) Cram, 1924; *Trichonema montgomeryi* (Boulenger, 1920)

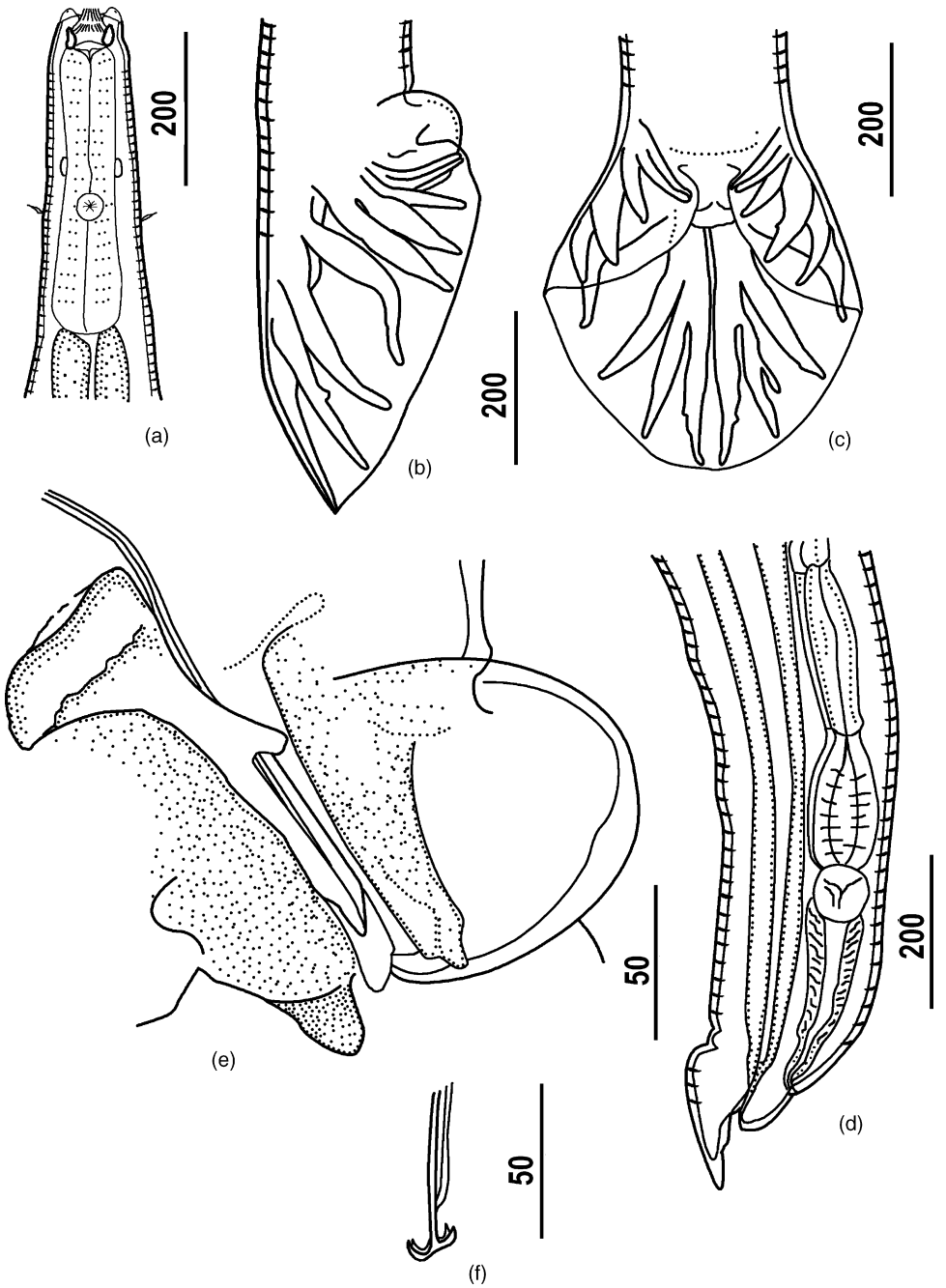

Fig. 33. *Cyathostomum montgomeryi*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Fused spicule tips of male.

Yorke and Maplestone, 1926; *Erschowinema montgomeryi* (Boulenger, 1920) Tschoijo, 1957.

General. ELC consists of 18 slender pointed leaves; ILC of 36 similar leaves at 1/2 of BC depth. Base of ILC located more deeply laterally than dorsoventrally. BC characterized by peculiar bilateral symmetry, dorsal and ventral walls considerably longer than lateral walls; absence of radial symmetry making optical section of head in lateral view different from ventral view. Buccal cavity depth and width nearly equal in lateral view, but dorsoventrally, buccal capsule nearly twice as wide as deep. Junction of S and BC without narrow constriction.

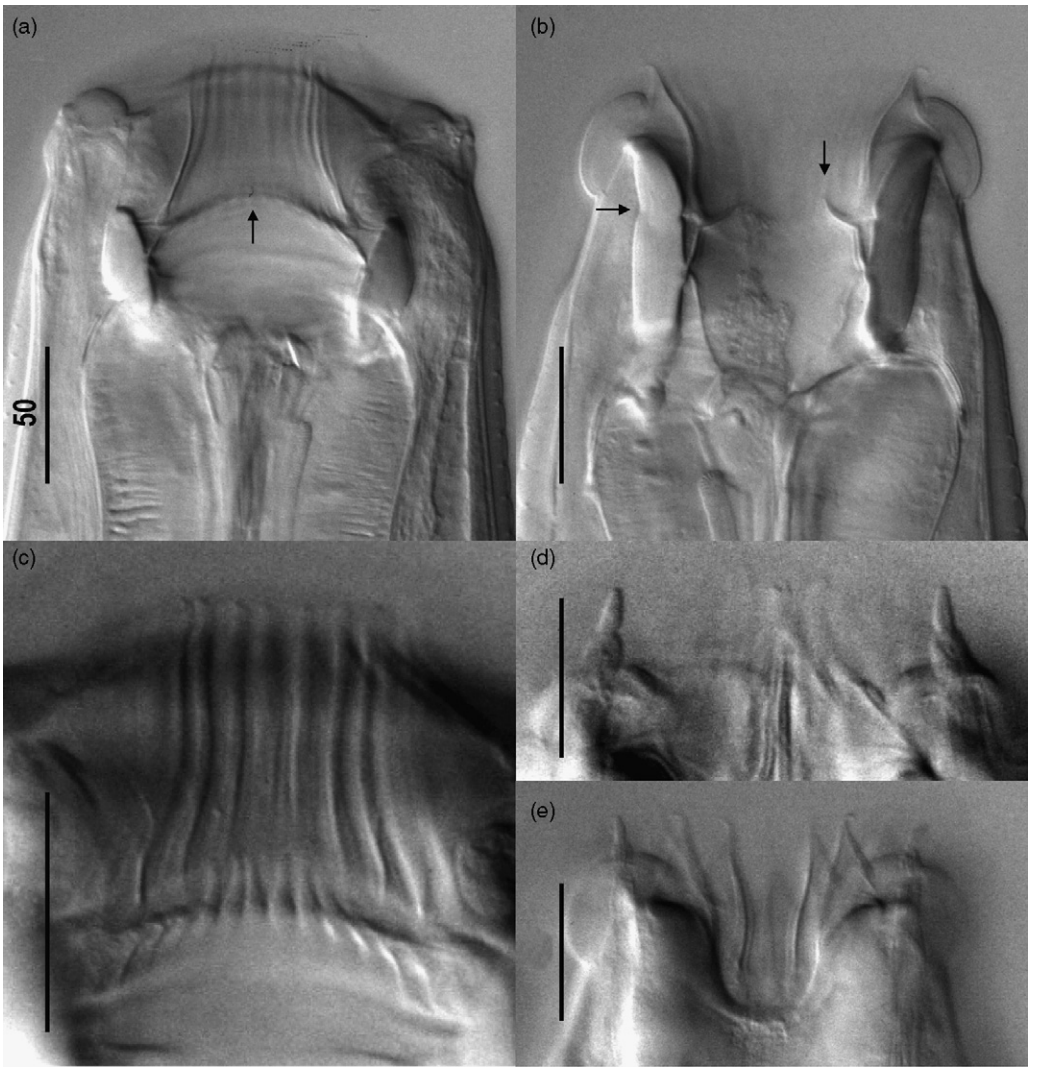

Fig. 34. *Cyathostomum montgomeryi*. (a) Buccal capsule, dorsoventral view, showing insertion line for elements of ILC and its junction with the ELC (arrow). (b) Buccal capsule, lateral view. Vertical arrow marks anterior tip of ILC and horizontal arrow marks junction of wall of BC and large support for ELC. (c) Elements of ELC and ILC. (d) Submedian papillae. (e) Wall of BC, lateral view, showing large gap in the large support for the ELC.

Support more developed on dorsal and ventral sides of buccal capsule; reaching to $^{1}/_{2}$–$^{2}/_{3}$ of height of walls of BC.

Male. Body length 6.05–7.28 mm. Body width 258–315. Esophagus length 300–370. NR 138–229, excretory pore 256–321, deirids 300–328 from anterior end. BC width 53–66, depth 33–44. Spicule length 540–642. Gubernaculum length 114–166. Dorsal ray length (from distal tip to origin of externodorsal ray) 261–400. Ventral rays length equal to laterals. Dermal collar poorly developed on ventral side of genital cone. Appendages of genital cone paired, hardly distinguishable oval projections. Protrusions of dermal collar absent.

Female. Body length 6.62–8.68 mm. Body width 284–442. Esophagus length 353–454. NR 187–240, excretory pore 240–334, deirids 307–328 from anterior end. BC width 55–80, depth 34–47. Vulva to tail tip 180–252. Anus to tail tip 66–120.

Hosts. *E. caballus*, *E. caballus* × *E. asinus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Africa.

6.1.6. *C. pateratum (Yorke and Macfie, 1919) Cram, 1924 (Figs. 35 and 36)*

Synonyms. *Cylicostomum pateratum* Yorke and Macfie, 1919; *Trichonema pateratum* (Yorke and

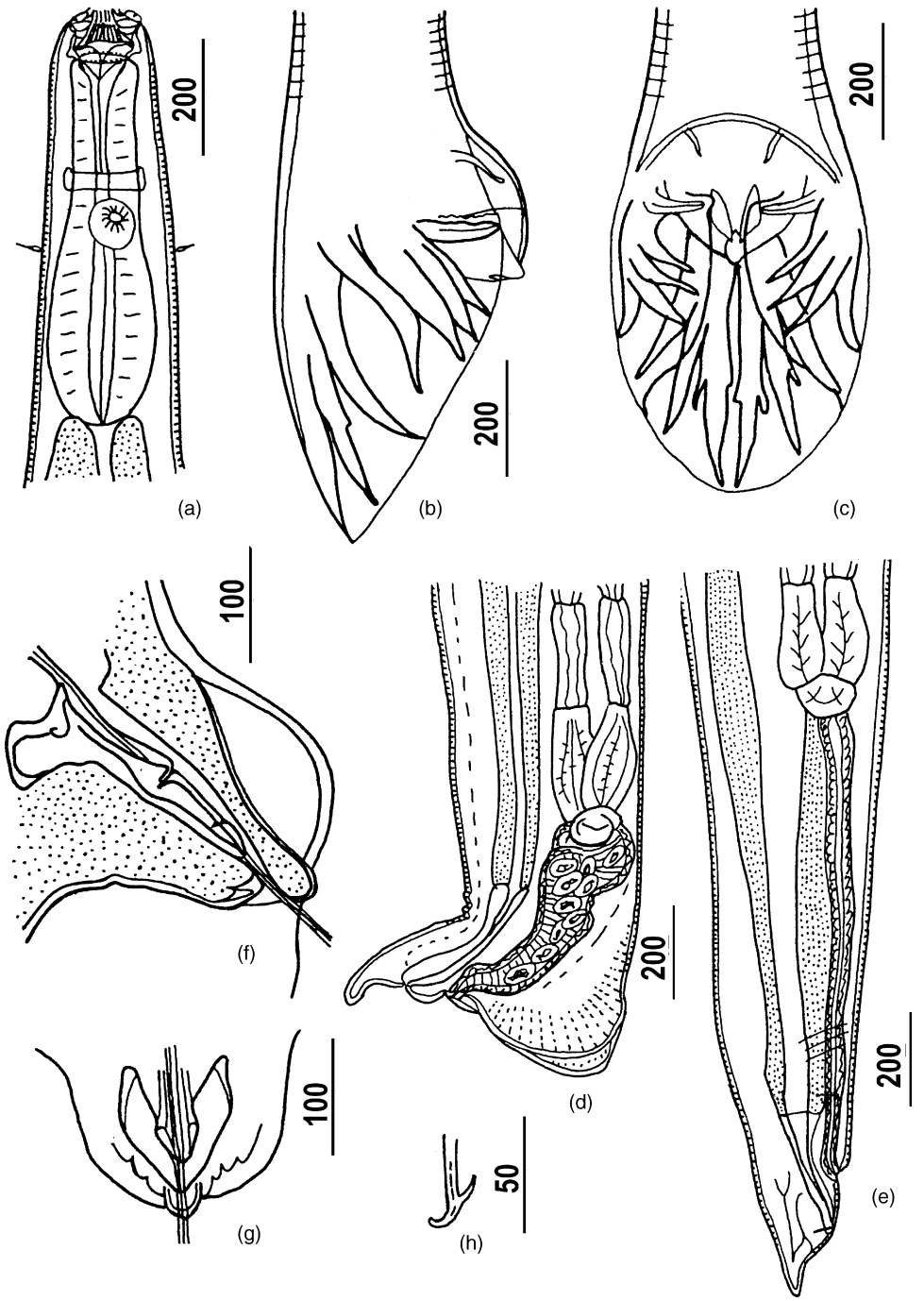

Fig. 35. *Cyathostomum pateratum*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) and (e) Tails of females, showing variations that may be due to maturity of specimen. (f) Genital cone, lateral view. (g) Tip of genital cone, ventral view. (h) Fused spicule tips of male (from Dvojnos and Kharchenko, 1994).

Macfie, 1919) Le Roux, 1924; *Cylicocercus pateratus* (Yorke and Macfie, 1919) Cram, 1924; *Cylicodontophorus pateratus* (Yorke and Macfie, 1919) Ershov, 1939; *Cylicostomum cymatostomum* Kotlán, 1919.

General. ELC with 20–24 elements; ILC with 40. Insertion point for posterior ends of elements of ILC about 1/2 of BC depth. Line formed by insertion of elements of ILC sinuous. Deirids near

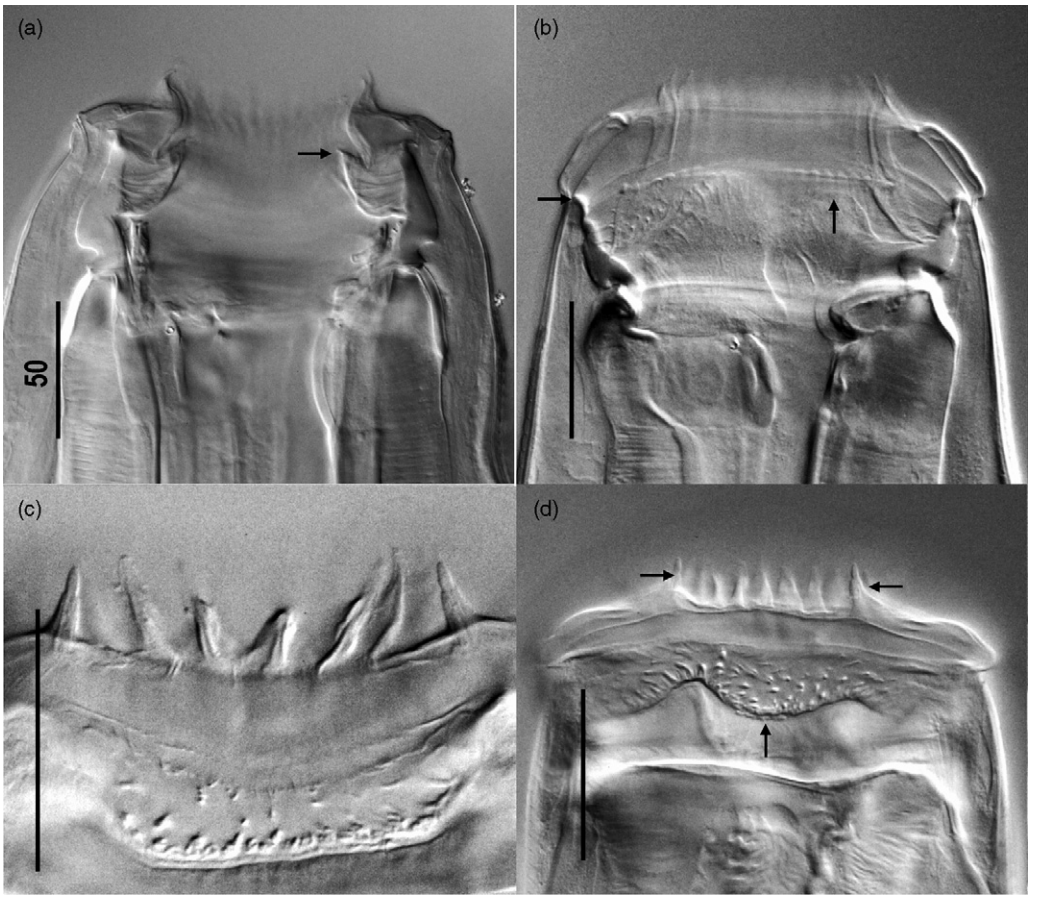

Fig. 36. *Cyathostomum pateratum*. (a) Buccal capsule, dorsoventral view. Arrow at tip of element of ILC. (b) Buccal capsule, lateral view. Vertical arrow marks tips of elements of ILC; horizontal arrow marks support for ELC. (c) Submedian papillae, elements of ELC and part of sinuous line of insertion for ILC. (d) Submedian papillae (horizontal arrows), elements of ELC and sinuous line of insertion for ILC (vertical arrow).

middle of glandular esophagus, 300–502 from anterior end.

Male. Body length 8–11 mm. Esophagus length 540–662. BC width 128–136, depth 38–46. Spicule length 1.67–1.86 mm. Gubernaculum length 200–297. Dorsal ray length (from distal tip to origin of externodorsal ray) 391–420. Ventral rays markedly shorter than laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone variable; studied specimens have number of oval projections similar to those of *C. catinatum*. Protrusions of dermal collar absent.

Female. Body length 8.4–13.0 mm. Esophagus length 620–770. BC width 100–140, depth 32–40. Vagina length 360–400. Vulva to tail tip 220–283. Anus to tail tip 105–140. Egg size 90–100 × 400–450.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.1.7. Discussion

The validity of the genus *Cyathostomum* and its type species *C. tetracanthum* have had a contentious history (Lichtenfels, 1975; Gibbons and Lichtenfels, 1999). The validity of *Cyathostomum* and its type species were finally established recently by the International Commission on Zoological Nomenclature (ICZN) (Opinion 1972 on Case 3075, June 2001). A few highlights of the history of the controversy and its solution are summarized here. Molin (1861) established *Cyathostomum* with *Strongylus tetracanthus* as the type species by monotypy. Looss (1900) recognized that Molin's *C. tetracanthum* included several species and restricted the name to the most common species found by him in Egypt. Railliet (1923) proposed that *Cyathostomum* was a homonym of *Cyathostoma* Blanchard, 1849 and established *Trichonema* Cobbold, 1874. For many years both *Trichonema* and *Cyathostomum* were used for overlapping groups of species. McIntosh (1951) established that *Cyathostomum* was not a homonym

and listed a synonymy of the type species. Lichtenfels (1975) reviewed the history of the controversy and followed McIntosh's recognition of *Cyathostomum*, with *C. tetracanthum* as the type species. Hartwich (1986) discovered Mehlis (1831) type series of *C. tetracanthum* and determined that the species designated by Looss (1900) as *C. tetracanthum* is not present among Mehlis' specimens. Hartwich selected and renamed *C. catinatum* Looss, 1900 as the true *C. tetracanthum* and renamed Looss' *C. tetracanthum* as *C. aegyptiacum*. In the interest of stability, the Sun City Workshop (Lichtenfels et al., 1998) voted (with the concurrence of Dr. Gerhard Hartwich) to ask the International Commission on Zoological Nomenclature to validate the names of these species in use prior to Hartwich's proposal (Gibbons and Lichtenfels, 1999). Only Dvojnos and Kharchenko (1994) had followed Hartwich and referred to *C. catinatum* as *C. tetracanthum*. The ICZN ruled (Opinion, 1972, 2001) "Ruling

(1) Under the plenary power all previous fixations of' type specimens for the nominal species *Strongy1us tetracanthus* Mehlis, 1831 are hereby set aside and the specimen no. 087757.00 in the U.S. National Parasite Collection, Beltsville, Maryland, collected by A. Looss in 1899, is designated as the neotype.
(2) The name *Cyathostomum* Molin, 1861 (gender: neuter), type species by monotypy *Strongy1us tetracanthus* Mehlis, 1831, is hereby placed on the Official List of Generic Names in Zoology.
(3) The following names are hereby placed on the Official List of Specific Names in Zoology:
  (a) *tetracanthus* Mehlis, 1831, as published in the binomen *Strongylus tetracanthus* and as defined by the neotype designated in (1) above (specific name of the type species of *Cyathostomum* Molin, 1861),
  (b) *catinatum* Looss, 1900, as published in the binomen *Cyathostomum catinatum*.
(4) The following names are hereby placed on the Official Index of Rejected and Invalid Generic Names in Zoology:
  (a) *Cylichnostomum* Looss, 1901 (a junior objective synonym of *Cyathostomum* Molin, 1861),
  (b) *Cylicostomias* Railliet, 1901 (a junior objective synonym of *Cyathostomum* Molin, 1861).
(5) The following names are hereby placed on the Official Index of Rejected and Invalid Specific Names in Zoology:
  (a) *hexacanthum* Wedl, 1856, as published in the binomen *Sclerostoma hexacanthum* (a junior objective synonym of *Strongy1us tetracanthus* Mehlis, 1831
  (b) *aegyptiacum* Railliet, 1923, as published in the binomen *Trichonema aegyptiacum* and as defined by the lectotype designated by Gibbons and Lichtenfels (1999) (a junior objective synonym of *Strongylus tetracanthus* Mehlis, 1831)."

Lichtenfels (1975) expanded McIntosh's (1951) concept of *Cyathostomum* to include nine species. Hartwich (1986) moved four of the nine species to a new genus, *Coronocyclus*. We (Lichtenfels et al., 1998) agreed with Hartwich's establishment of *Coronocyclus* and now include only five species in *Cyathostomum*.

6.2. *Coronocyclus Hartwich, 1986*

General. Medium-sized Cyathostominea. MC inflated, high, ring-shaped, divided into inner and outer rings. Posterior edge of MC situated anterior to edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae bulbous or bullet-shaped, two to three times as long as thick. Stalk of submedian papillae longer than broad. ELC markedly less numerous and longer than ILC. Elements of ELC longer than broad, tips pointed; insertion point on tips of elements of ILC. Elements of ILC longer than broad, tips pointed; insertion point about $^1/_4$–$^1/_2$ of BC depth. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC separate from BC, elongate, spindle-shaped. Septum intracoronare absent. Walls of BC straight, without ring-like thickening. Buccal cavity cylindrical, wider than deep. Dorsal gutter nipple-, or button-, or tongue-like. Buccal teeth absent. Esophageal funnel shallow. Esophageal teeth prominent or not. Anterior muscular portion of esophagus about $^1/_4$–$^1/_3$ of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches. Ventral rays shorter or of equal length to laterals. Dorsal lobe longer then lateral lobes. Externodorsal rays origin at junction of dorsal and laterals rays. Gubernaculum large, with dorsal handle and ventral notch. Genital cone short, conical. Spicule tips pick-shaped.

Female. Vulva about one tail length from anus. Vagina shorter or longer than ovejector sphincter. Ovejector vestibule oval or Y-shaped; infundibulum equal to or longer than sphincter. Tail digitiform, short, length less than 2× diameter at anus.

Type species. *C. coronatus* (Looss, 1990) Hartwich, 1986

6.2.1. Key to species of Coronocyclus

(1) a. Optical section of wall of buccal capsule with medial bend near middle of cylinder; dorsal gutter not evident; dorsal ray twice as long as lateral rays of copulatory bursa	2
b. Buccal capsule wall without medial bend near middle; dorsal gutter prominent; dorsal ray only slightly longer than lateral rays of copulatory bursa	3
(2) a. ILC inserted at 1/3 of BC depth; proximal branch of dorsal ray does not overlap origin of middle branch	*C. sagittatus*
b. ILC inserted at 1/5–1/4 of BC depth; proximal branch of dorsal ray overlaps origin of middle branch	*C. coronatus*
(3) a. Mouth collar high, dorsal, ventral and lateral depressions form four lips; dorsal gutter short, broad, straight, nipple-like	*C. labiatus*
b. Mouth collar not prominent; dorsal gutter tongue-like, projects into buccal cavity	4
(4) a. BC lateral walls thickest near middle of cylinder, ventral wall slightly thicker posteriorly; tongue-like dorsal gutter smaller than dorsal esophageal tooth	*C. labratus*
b. All aspects of BC wall thicker posteriorly; tongue-like dorsal gutter larger than dorsal esophageal tooth	*C. ulambajari*

6.2.2. *C. coronatus* (Looss, 1900) Hartwich, 1986 (Figs. 37 and 38)

Synonyms. *Cyathostomum coronatum* Looss, 1900; *Cylichnostomum coronatum* (Looss, 1900) Looss, 1902; *Cylicostomum coronatum* (Looss, 1900) Gedoelst, 1903; *Trichonema coronatum* (Looss, 1900) Le Roux, 1924; *Cylicostomias coronata* (Looss, 1900) Cram, 1925; *Erschowinema coronatum* (Looss, 1900) Tschoijo, 1957; *Trichonema subcoronatum* Yamaguti, 1943.

General. Tip of submedian papillae bulbous, twice as long as thick. ELC with 20–22 long, pointed, leaf-like elements; ILC with 72–80 shorter, thin, palisade-like elements. ILC inserted at 1/5–1/4 of BC depth; proximal branch of dorsal ray overlaps origin of middle branch. Support for ELC separate from BC, elongate, spindle-shaped. Optical section of wall of buccal capsule with medial bend near middle of cylinder. Dorsal gutter not evident. Esophageal teeth not prominent.

Male. Body length 6.8–10.3 mm. Esophagus length 360–520. BC width 62–92, depth 32–40. Distance from deirids to head end 320–376. Spicule length 0.72–1.35 mm. Gubernaculum length 156–210. Dorsal ray length 502–717. Ventral rays length equal to laterals. Appendages of genital cone in form of two oval formations, fused at medial line with numerous setae similar to *C. longibursatus* and *C. agittatus*.

Female. Body length 7.5–10.5 mm. Esophagus length 400–683. BC width 68–126, depth 38–44. Anterior end to deirids 352–450. Vulva to tail tip 224–315. Anus to tail tip 150–223. Vagina length 280–360. Egg size 92–103 × 44–55. Sublateral protrusions near vulva undeveloped. Vagina longer than sphincter of ovejector. Infundibulum length about equal to sphincter length.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.2.3. *C. labiatus* (Looss, 1902) Hartwich, 1986 (Figs. 39 and 40)

Synonyms. *Cyathostomum labiatum* (Looss, 1902) McIntosh, 1933; *Cyathostomum labratum* Looss, 1900, in part; *Cylichnostomum labiatum* Looss, 1902; *Cylicostomum labiatum* (Looss, 1902) Gedoelst, 1903; *Cylicostomum labiatum digitatum* Ihle, 1921; *Trichonema labiatum* (Looss, 1902) Le Roux, 1924; *Cylicostomias labiatum* (Looss, 1902) Cram, 1925; *Schulzitrichonema labiatum* (Looss, 1902) Baruš, 1961.

General. MC high, dorsal, ventral and lateral depressions form four lips. Tip of submedian papillae bullet-shaped. ELC with 18–19 elements; ILC with 40–52. Insertion point for posterior ends of elements of ILC about 1/2 of BC depth. Support for ELC elongate, curving, spindle-shaped. Buccal capsule wall short, thicker in middle, without medial bend near middle. Dorsal gutter short, thick, nipple-like. Esophageal teeth not prominent. Deirids near middle of glandular esophagus, 300–403 from anterior end.

Male. Body length 7–9 mm. Esophagus length 360–390. BC width 40–56, depth 12–16 to 20–28. Spicule length 1.13–1.43 mm. Gubernaculum length 160–204. Dorsal ray length 358–387. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone consists of two pairs of conical projections. Protrusions of dermal collar paired, located close to appendages of genital cone.

Female. Body length 9.5–11.0 mm. Esophagus length 430. BC width 40–56, depth 12–16 to 20–28. Vulva to tail tip 160–220. Anus to tail tip 45–89. Egg size 76–80 × 32–38. Vagina longer than sphincter of ovejector; infundibulum longer than sphincter.

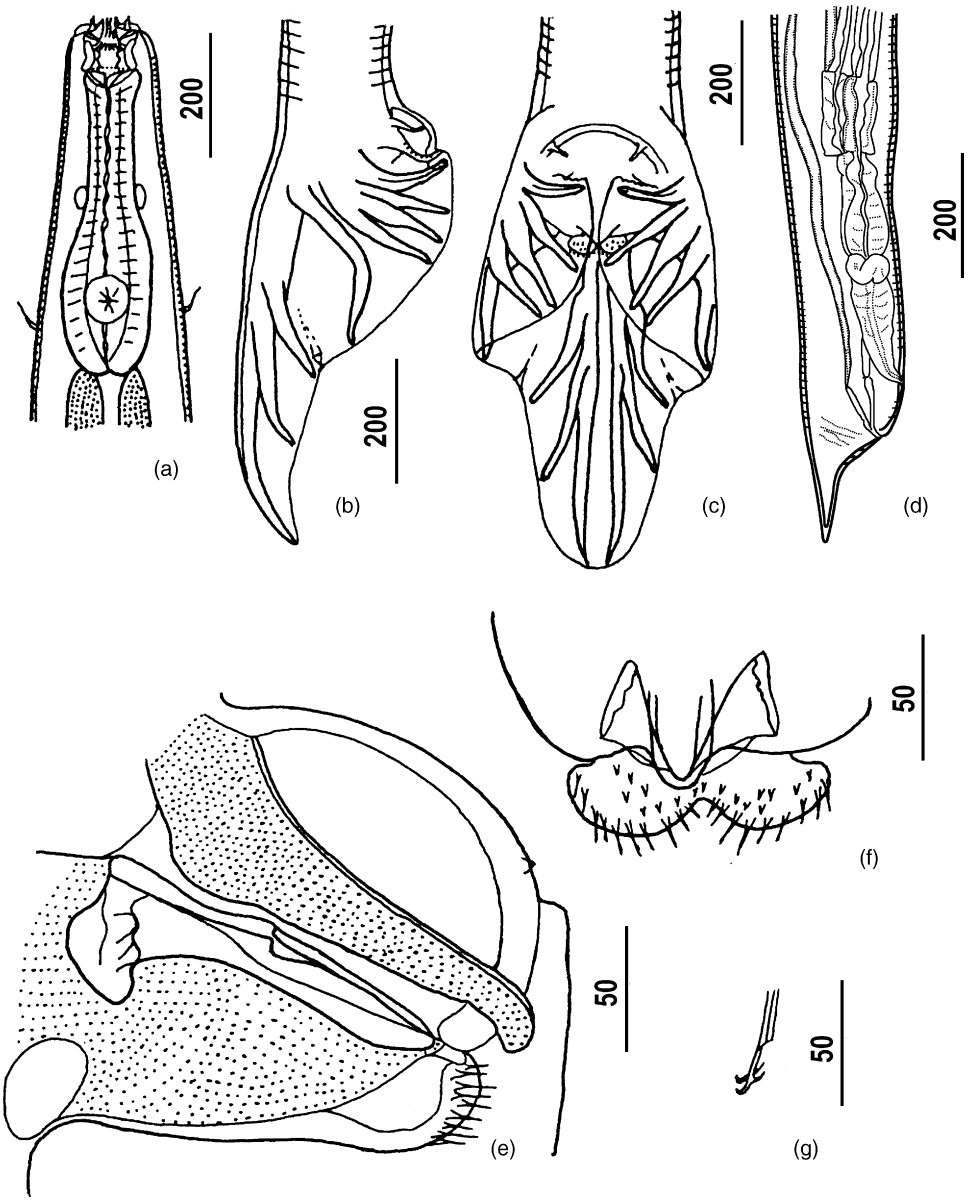

Fig. 37. *Coronocyclus coronatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.2.4. C. labratus (Looss, 1900) Hartwich, 1986 (Figs. 41 and 42)

Synonyms. *Cyathostomum labratum* Looss, 1900; *Cylichnostomum labratum* (Looss, 1900) Looss, 1902; *Cylicostomum labratum* (Looss, 1900) Gedoelst, 1903; *Trichonema labratum* (Looss, 1900) Le Roux, 1924; *Cylicostomias labrata* (Looss, 1900) Cram, 1925; *Schulzitrichonema labratum* (Looss, 1900) Baruš, 1962.

General. Mouth collar not prominent. Tip of submedian papillae bullet-shaped. ELC with 18 elements; ILC with 48–54. Support for ELC elongate, thin, pyriform with thicker distal end. BC wall without medial bend near middle. BC lateral walls thickest near middle of cylinder; ventral wall slightly thicker posteriorly. Dorsal esophageal tooth prominent. Ton-

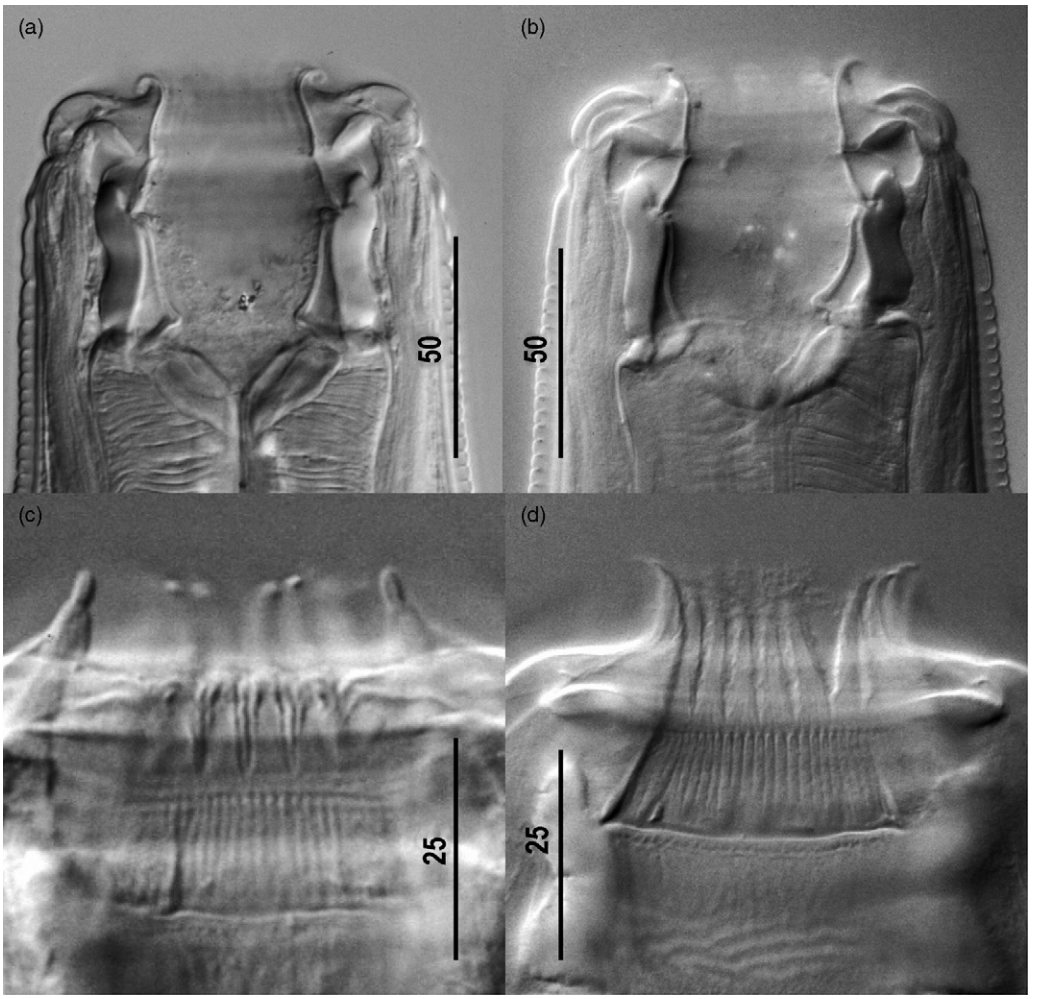

Fig. 38. *Coronocyclus coronatus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Submedian papillae, elements of ILC and ELC. (d) Elements of ILC and ELC.

gue-like dorsal gutter smaller than dorsal esophageal tooth. Deirids and excretory pore 240–280 from anterior end.

Male. Body length 5.4–8.0 mm. Esophagus length 336–401. BC depth 20–26, width 44–52. Spicule length 0.83–1.12 mm. Gubernaculum length 120–132. Dorsal ray length (from distal tip to origin of externodorsal ray) 330–387. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone paired, pear-shaped, fused medially. Protrusions of dermal collar absent.

Female. Body length 7.3–9.5 mm. Esophagus length 400. BC depth 20–26, width 44–52. Vulva to tail tip 188. Anus to tail tip 71–96. Egg size 39–44 × 93–98. Tail straight, with thickened cuticle. Vagina longer than sphincter of ovejector; infundibulum longer than sphincter.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.2.5. *C. agittatus (Kotlán, 1920) Hartwich, 1986 (Figs. 43 and 44)*

Synonyms. *Cylicostomum sagittatum* Kotlán, 1920; *Trichonema sagittatum* (Kotlán, 1920) Le Roux, 1924; *Cylicostomias sagittatum* (Kotlán, 1920) Cram, 1925; *Cylicodontophorus sagittatum* (Kotlán, 1920) Ershov, 1939.

General. Tip of submedian papillae bulbous; twice as long as thick. ELC with 16–20 elements; ILC 60–80. Insertion point for posterior ends of elements of ILC about 1/3 of BC depth. Support for ELC elongate, spindle-shaped. Optical section of wall of buccal

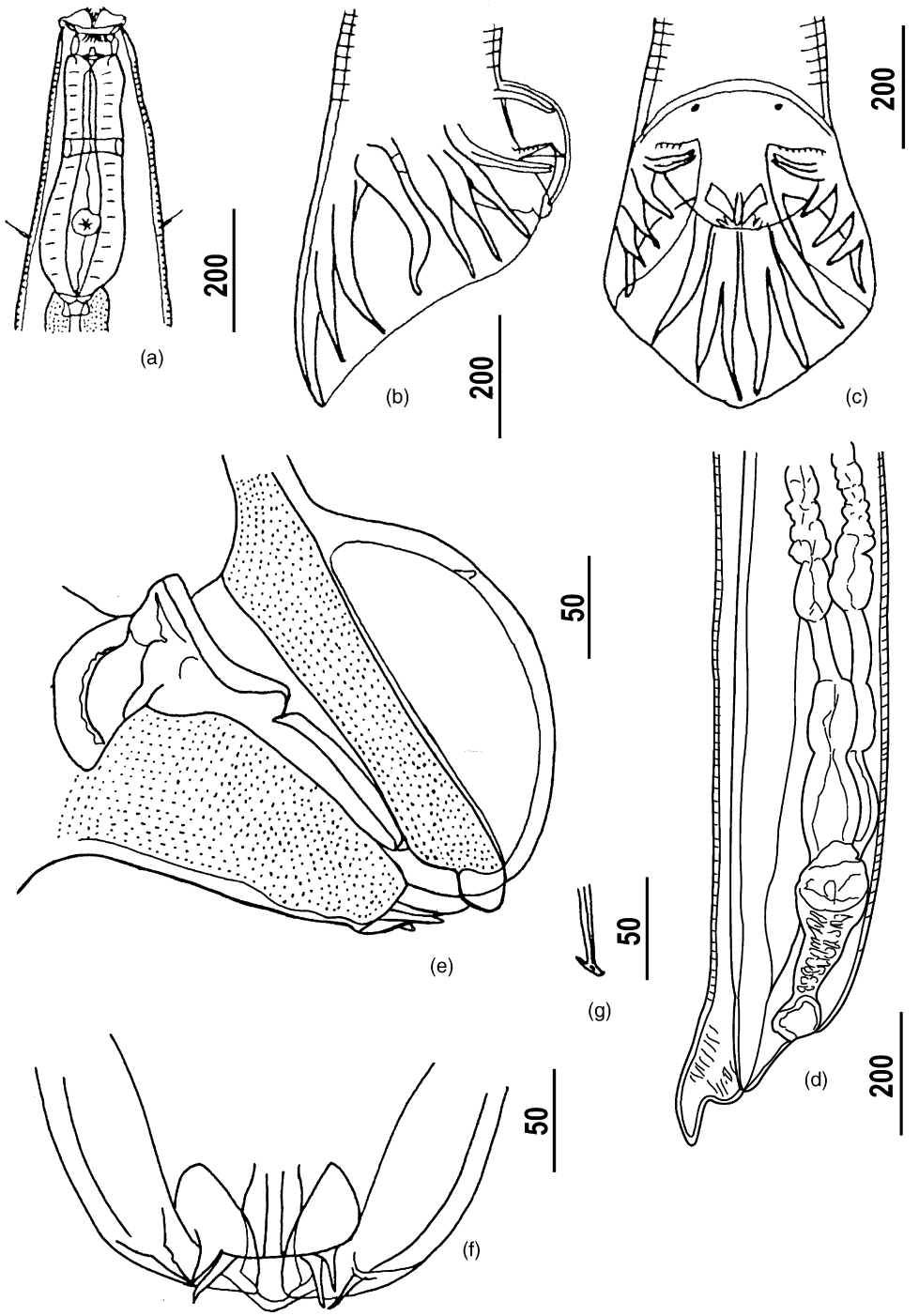

Fig. 39. *Coronocyclus labiatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

capsule with medial bend near middle of cylinder. Esophageal teeth not prominent. Anterior end to: deirids 422–524; excretory pore 384–486.

Male. Body length 9.5–11.0 mm. Esophagus length 541–620. BC width 146–160, depth 32–36. Spicule length 1.0–1.42 mm. Gubernaculum length 180–239. Dorsal ray length (from distal tip to origin of externodorsal ray) 420. Ventral rays length equal to laterals. Dermal collar absent. Appendages of genital cone paired, oval, separated formations with numerous

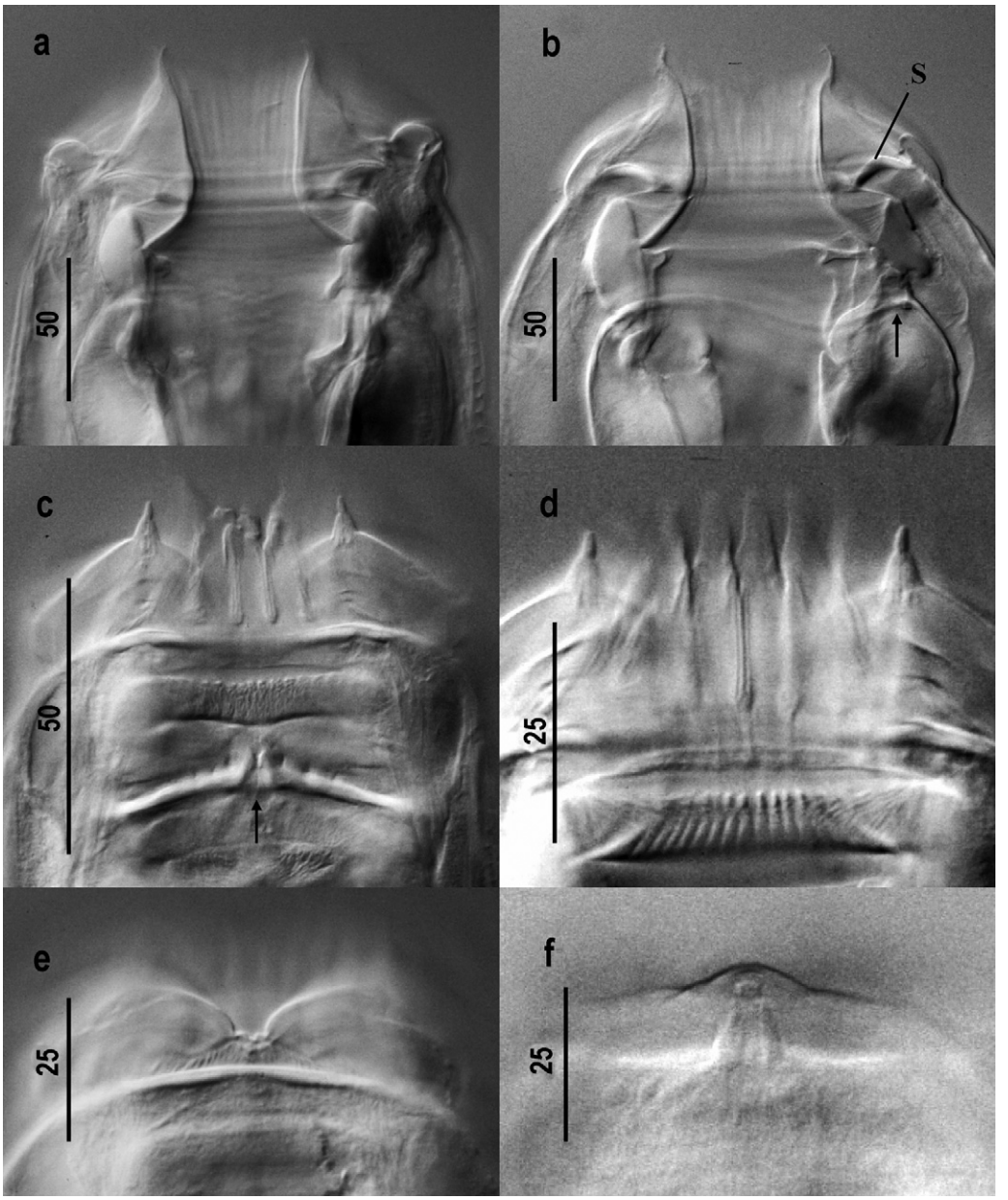

Fig. 40. *Coronocyclus labiatus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing supports (s), dorsal gutter (arrow) and cuticular formed by lining of BC. (c) Submedian papillae, elements of ILC and ELC and dorsal gutter (arrow). (d) Submedian papillae, elements of ILC and ELC. (e) Ventral notch (also present dorsally) between swellings of mouth collar. (f) Lateral papilla.

setaceous protrusions; like *C. coronatus*. Protrusions of dermal collar absent.

Female. Body length 10.5–12.8 mm. Esophagus length 620–730. BC width 96–128, depth 33–40. Vulva to tail tip 280–460. Anus to tail tip 140–240. Egg size 86–94 × 44–50. Tail of mature females straight, tip pointed. Sublateral protrusions poorly developed. Vagina longer than sphincter of ovejector. Infundibulum about equal to sphincter.

Hosts. *Equus caballus*, *E. caballus* × *E. asinus*, *E. przewalskii*.

Locality. Colon.

Distribution. Europe, Asia.

6.2.6. *C. ulambajari* Dvojnos et al., 1994 (Figs. 45 and 46)

General. MC not prominent. Tip of submedian papillae bullet-shaped, less than twice as long as thick.

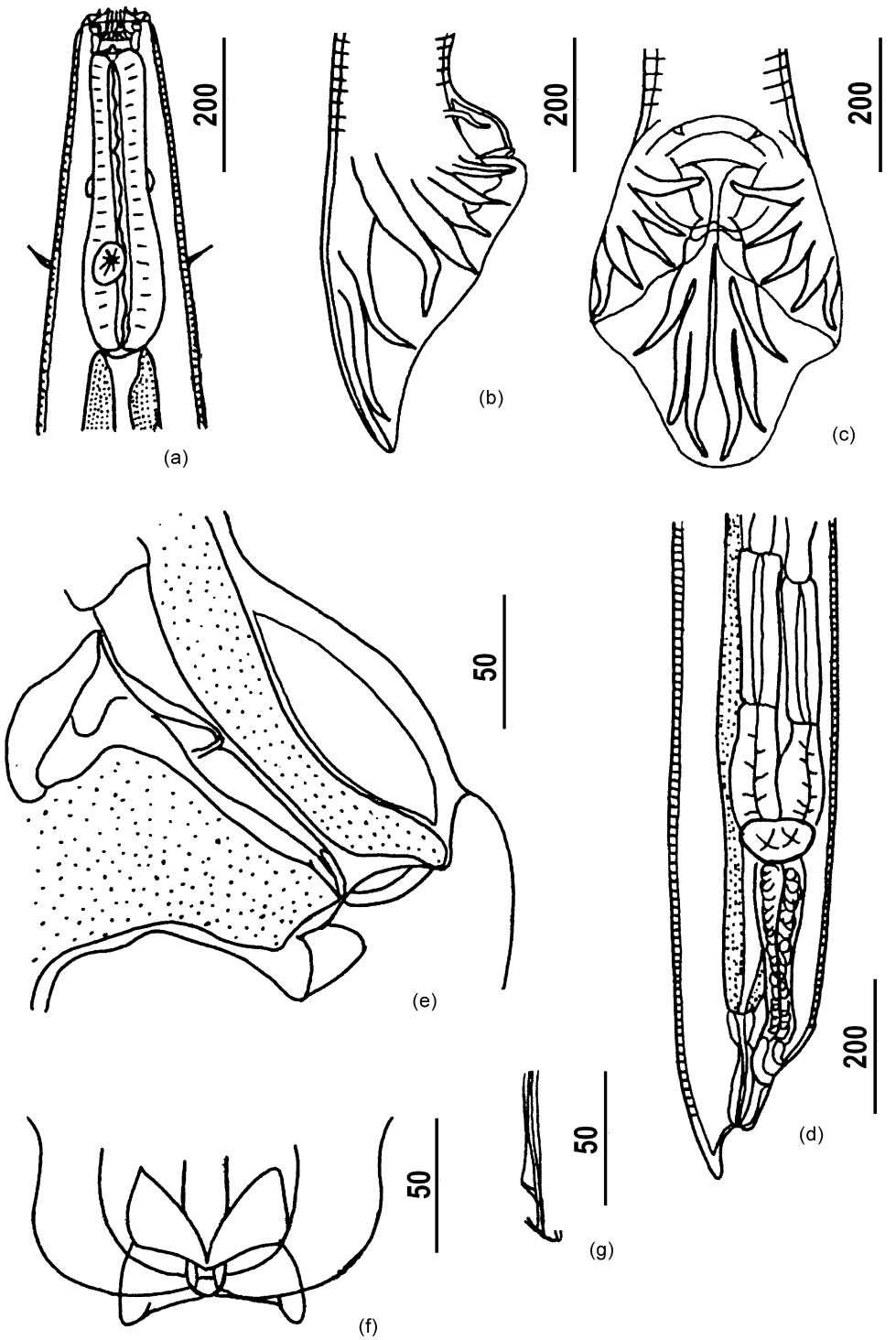

Fig. 41. *Coronocyclus labratus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (from Dvojnos and Kharchenko, 1994).

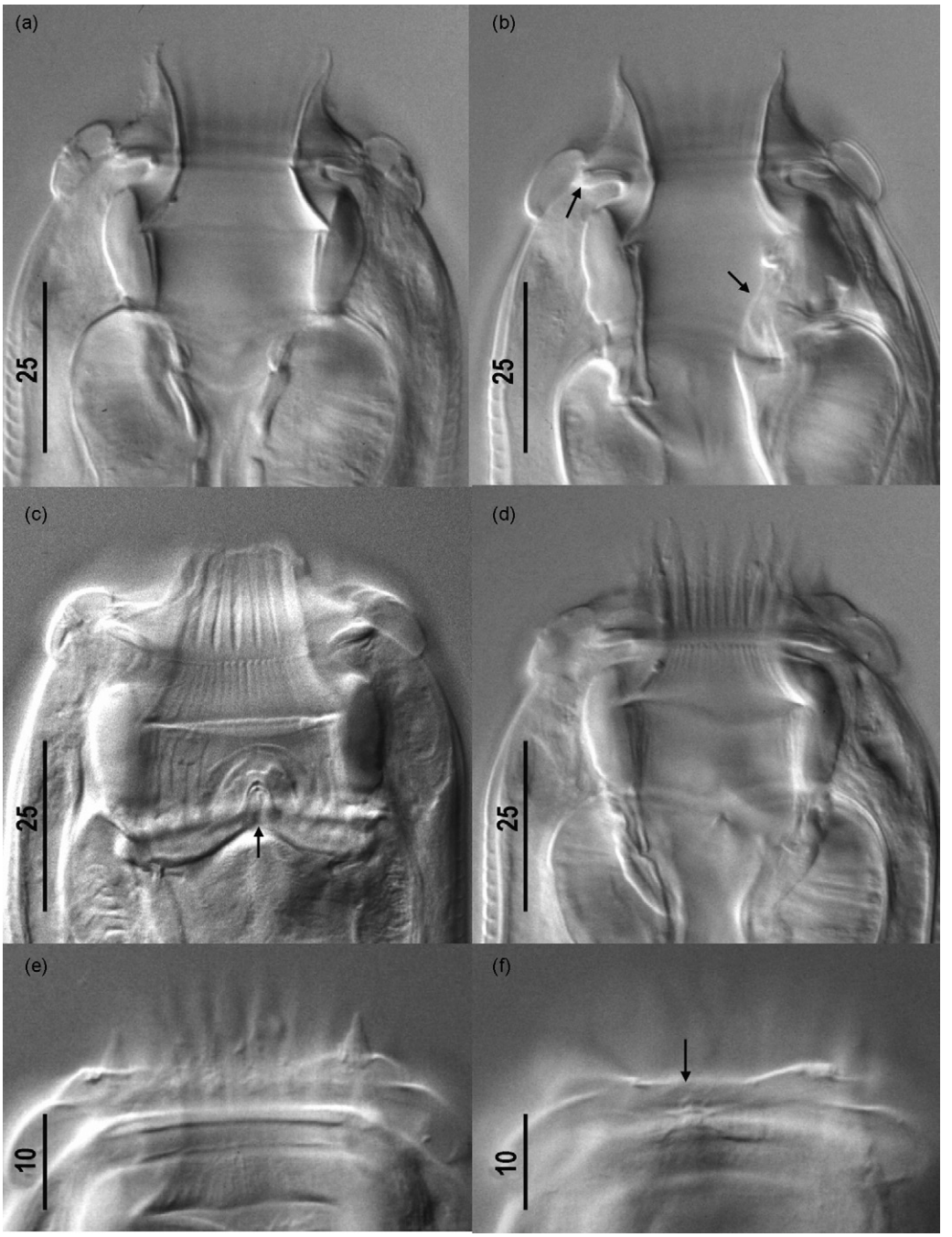

Fig. 42. *Coronocyclus labratus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing support (upper arrow) and dorsal gutter (lower arrow). (c) Elements of ILC and ELC and dorsal gutter (arrow). (d) Buccal capsule, lateral view, showing elements of ILC and ELC. (e) Submedian papillae and elements of ILC. (f) Lateral papilla (arrow).

ELC with 28 elements; ILC with approximately 80. Insertion point for ILC about 1/5 of BC depth. Support separate from BC, elongate, curving, spindle-shaped. Buccal capsule wall thickest posteriorly, without medial bend near middle. Tongue-like dorsal gutter larger than dorsal esophageal tooth. Dorsal esophageal tooth prominent.

Male. Body length 7.7–8.7 mm. Esophagus length 504–509. BC width 100–105, depth 30. Distance from anterior end to: EP 375–386; to deirids 420. Spicule

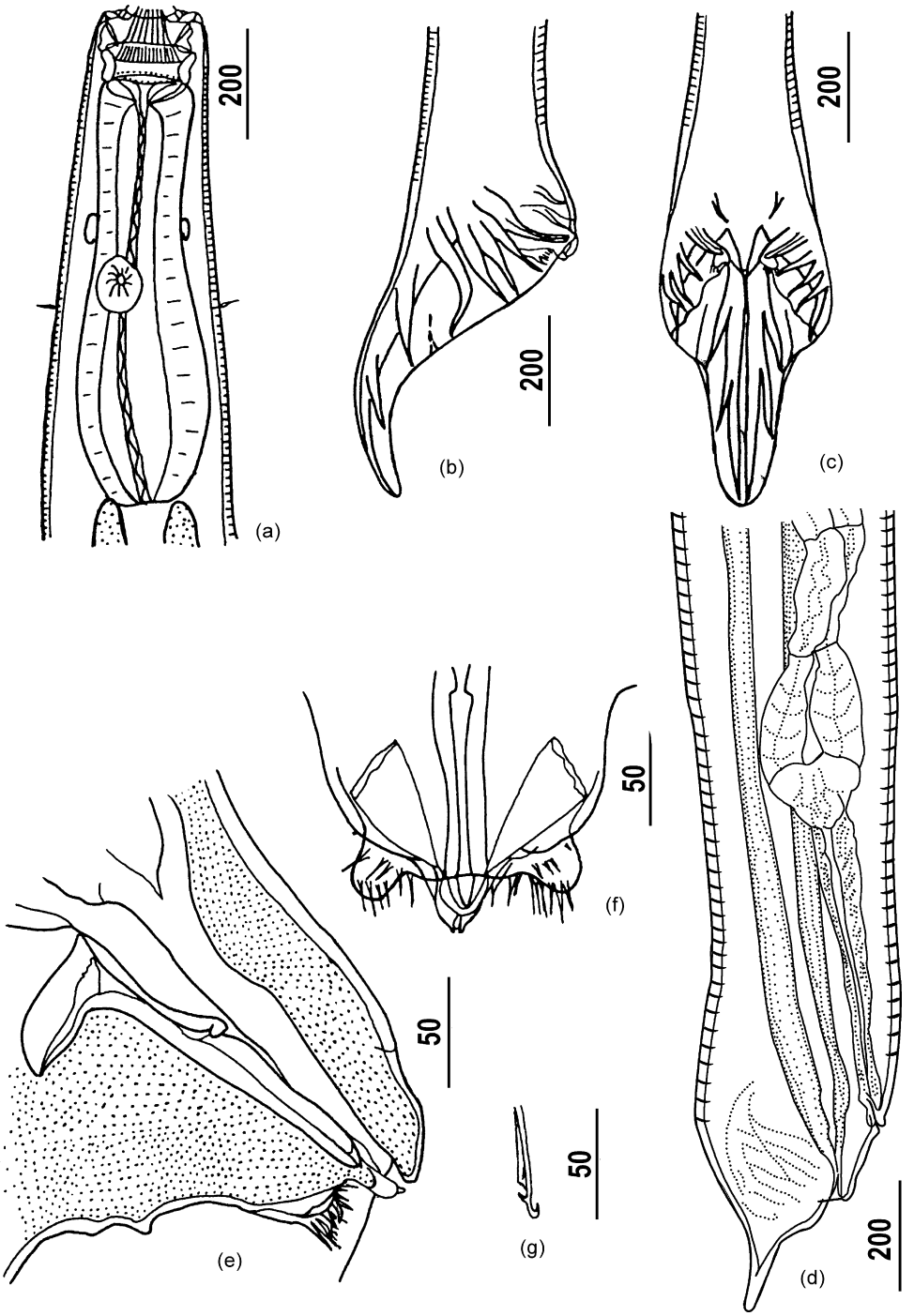

Fig. 43. *Coronocyclus sagittatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

length 1.04 mm. Gubernaculum length 276. Dorsal ray length 315–377. Dermal collar undeveloped. Appendages of genital cone small, conical.

Female. Body length 9.5–11.3 mm. Esophagus length 459–480. BC width 82–87, depth 27–28. Anterior end to: deirids 380–390; excretory pore 340–380. Vulva to tail tip 205–300. Anus to tail tip 81–147. Egg size 135–147 × 51–60. Vagina shorter than sphincter of ovejector. Infundibulum longer than sphincter.

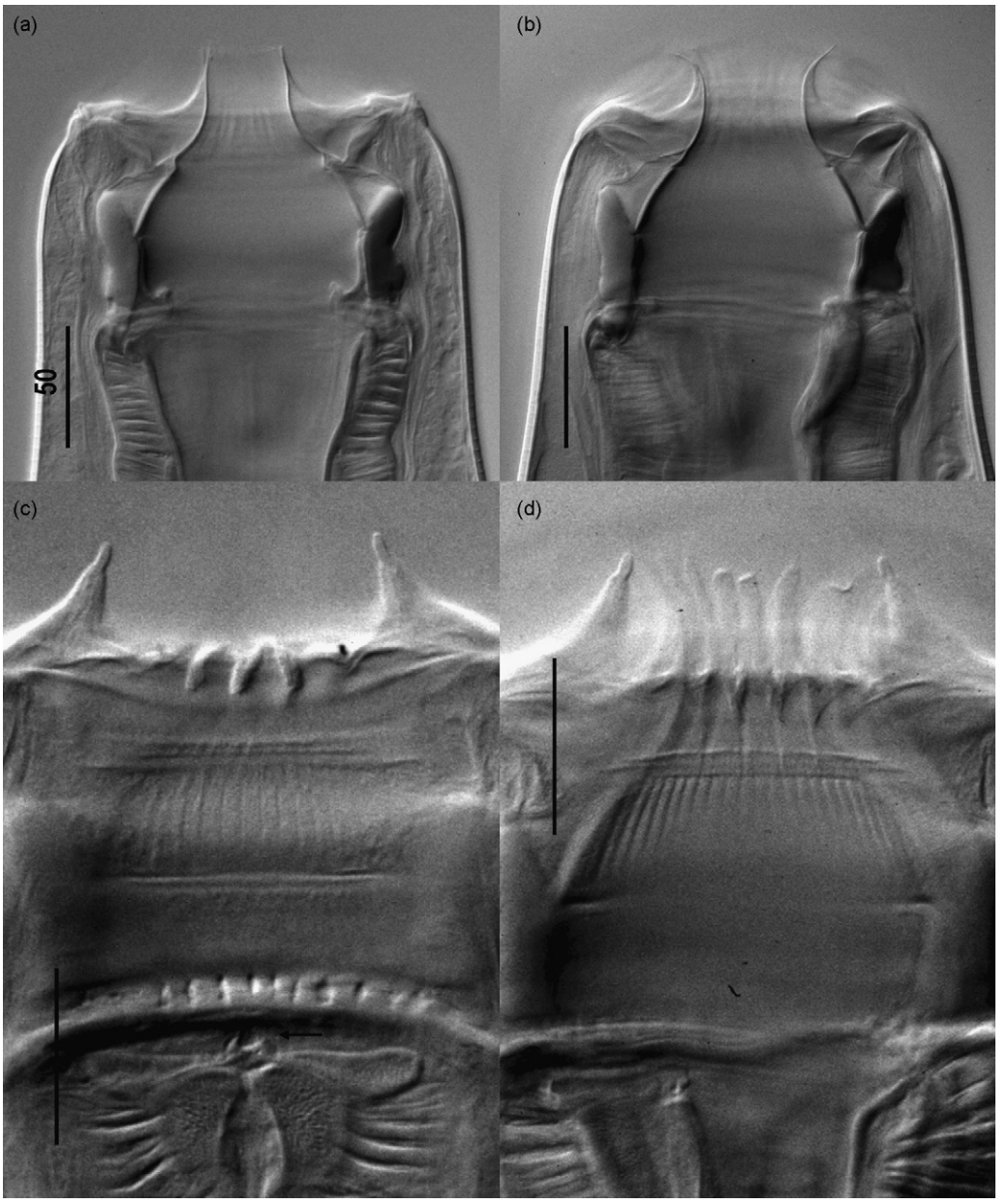

Fig. 44. *Coronocyclus sagittatus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Submedian papillae, elements of ILC and dorsal gutter. (d) Submedian papillae and elements of ILC and ELC.

Hosts. *Equus caballus*.
Locality. Cecum, colon.
Distribution. Asia.

6.2.7. Discussion

Hartwich (1986) erected *Coronocyclus* for four species with the support of the external leaf crown (ELC) separated anteriorly from the wall of the buccal capsule. The genus is characterized by a suite of characteristics and can be identified easily. Dvojnos et al. (1994) added *C. ulambajari* to this genus.

6.3. Cylicostephanus Ihle, 1922

Synonyms. *Cylicostomum* (*Cylicostephanus*) Ihle, 1922; *Cylicostomum* (*Cylicotetrapedon*) Ihle, 1925; *Erschowinema* Tschoijo, 1957.

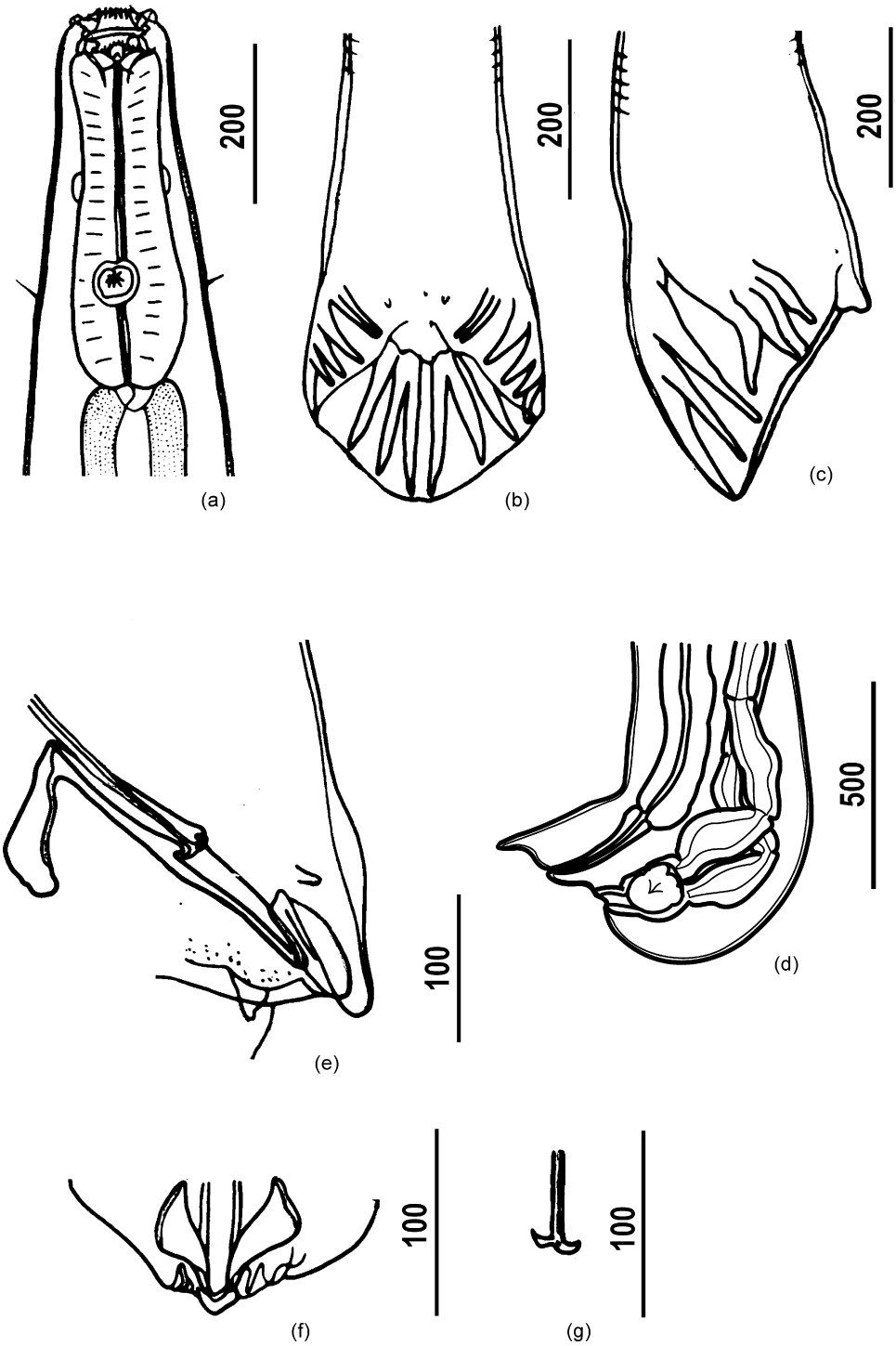

Fig. 45. *Coronocyclus ulambajari*. (a) Esophageal region, ventral view. (b) Male tail, dorsoventral view. (c) Male tail, lateral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

General. Small Cyathostominae. MC flattened, divided into inner and outer rings. Posterior edge of MC posterior to edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae spindle-, cone- or bullet-shaped, about two to three times as long as thick. Stalk of submedian papillae longer than broad. ELC markedly

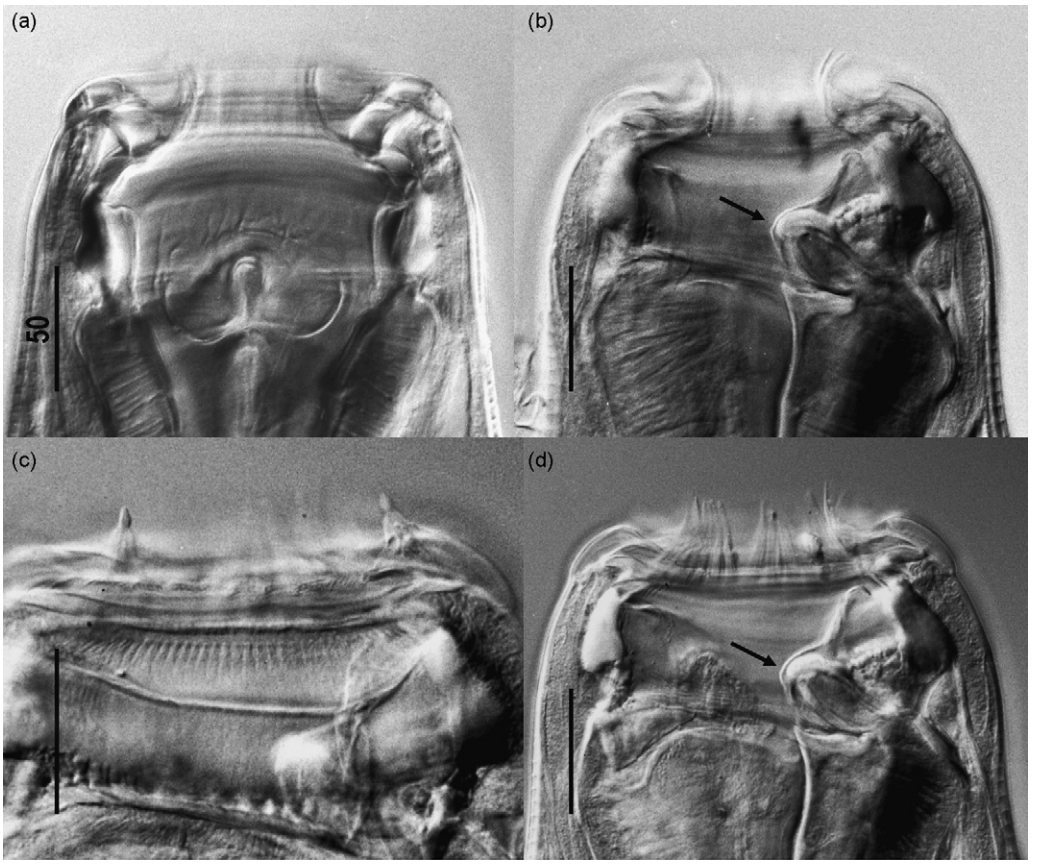

Fig. 46. *Coronocyclus ulambajari*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing tongue-like dorsal gutter (arrow). (c) Submedian papillae and elements of ILC. (d) Buccal capsule supports, elements of ILC and dorsal gutter (arrow), lateral view.

less numerous, or nearly equal in number, and longer than ILC. Elements of ELC longer than broad, tips rounded or pointed; insertion point on tips of ILC or slightly back from tips. Elements of ILC longer than broad, tips pointed or rounded; insertion point about 1/4 or less of BC depth. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, short, triangular in optical section. Septum intracoronare origin on support or BC. Medial insertion of septum intracoronare situated anterior to junction of ELC and ILC. Walls of BC straight or S-shaped, thicker posteriorly or anteriorly. Buccal cavity can be deeper than wide, as deep as wide or wider than deep, but wider posteriorly. Dorsal gutter button-like or elongate. Buccal teeth absent. Esophageal funnel shallow or enlarged. Esophageal teeth usually prominent. Anterior muscular portion of esophagus about 1/4−1/3 of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches. Ventral rays may have different length relative to laterals. Dorsal lobe longer then lateral lobes. Externodorsal rays origin at junction of dorsal and lateral rays. Gubernaculum large, with dorsal handle; ventral notch evident or inconspicuous. Genital cone short, conical. Spicule tips pick-shaped.

Female. Vulva about one, or less than one, tail length from anus. Vagina longer than sphincter of ovejector. Ovejector vestibule oval or Y-shaped. Tail conical or digitiform, short, length less than 2× diameter at anus.

Type species. *C. calicatus* (Looss, 1900) Cram, 1924.

6.3.1. Key to species of *Cylicostephanus*

(1) a. BC much deeper than broad	2
b. BC nearly as broad or broader than deep	3
(2) a. Elements of ELC triangular, number 8; submedian papillae notched at point one-half distance between tips and buccal collar	*C. minutus*

b. Elements of ELC digitiform, number 12–18; submedian papillae notched near tips	*C. calicatus*
(3) a. Walls of BC markedly thicker anteriorly than posteriorly; elements of ELC about as broad as long; dorsal gutter extends almost to base of ILC	4
b. Walls of BC of nearly uniform thickness; elements of ELC more than twice as long as broad; dorsal gutter extends slightly more than halfway or less toward base of ILC	5
(4) a. BC markedly asymmetrical in lateral view; walls of capsule concave; teeth in esophageal funnel not prominent. Submedian papillae tips pointed	*C. asymetricus*
b. BC nearly symmetrical; walls of capsule straight; prominent teeth in esophageal funnel. Submedian papillae tips bulbous	*C. bidentatus*
(5) a. In dorsal view, walls of BC straight, slightly thicker posteriorly; dorsal gutter slightly more than 1/2 as long as depth of BC	*C. hybridus*
b. In dorsal view, walls of BC with slight compound curve slightly thicker anteriorly; dorsal gutter button-like	6
(6) a. Elements of ELC and ILC in 1:1 ratio; dorsal ray of male bursa extremely long; female tail straight; teeth in esophageal funnel not prominent	*C. longibursatus*
b. Elements of ILC almost twice as numerous as elements of ELC; dorsal ray of male bursa not unusually long; female tail bent dorsally with a ventral prominence; prominent teeth in esophageal funnel	*C. goldi*

6.3.2. *C. calicatus (Looss, 1900) Cram, 1924 (Figs. 47 and 48)*

Synonyms. *Cyathostomum calicatum* Looss, 1900; *Cylichnostomum calicatum* (Looss, 1900) Looss, 1902; *Cylicostomum calicatum* (Looss, 1900) Gedoelst, 1903; *Trichonema calicatum* (Looss, 1900) Le Roux, 1924; *Erschowinema calicatum* (Looss, 1900) Tschoijo, 1957; *Cylicostomum barbatum* Smit and Notosoediro, 1923; *Trichonema tsengi* K'ung and Yang, 1963.

General. Tip of submedian papillae bullet-shaped, two times as long as thick. ELC with 12–18 elements; ILC with 26–42. Insertion for ELC on tips of elements of ILC. Tips of elements of ILC rounded. Insertion of ILC on anterior edge of BC. Septum intracoronare origin on support. Walls of BC straight, thicker posteriorly. Buccal cavity deeper than wide. Dorsal gutter elongate, more than 1/2 depth of BC. Deirids and excretory pore 281–358 and 217–358 from anterior end.

Male. Body length 5.1–7.1 mm. Esophagus length 289–356. BC width 30–36, depth 35–40. Spicule length 0.85–1.02 mm. Gubernaculum large, with dorsal handle and ventral notch; length 110–126. Dorsal ray length (from distal tip to origin of externodorsal ray) 400–0.502. Ventral rays shorter than laterals. Dermal collar well-developed around genital cone. Appendages of genital cone paired, separated, spherical formations with few projections that may be bifurcated.

Female. Body length 6.7–8.2 mm. Esophagus length 315–398. BC width 30–38, depth 36–43. Vagina length 320–400. Vulva to tail tip 160–228. Anus to tail tip 83–135. Egg size 57–69 × 37–45. Ovejector infundibulum length about equal to sphincter length. Tail of mature females conical, straight, tip pointed; sublateral protrusions poorly developed.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.3.3. *C. asymetricus (Theiler, 1924) Cram, 1925 (Figs. 49 and 50)*

Synonyms. *Cylicostomum asymetricum* Theiler, 1924; *Cylicotetrapedon asymetricum* (Theiler, 1924) Ihle, 1925; *Schulzitrichonema asymetricum* (Theiler, 1924) Ershov, 1943; *Erschowinema asymetricum* (Theiler, 1924) Tschoijo, 1957.

General. Tip of submedian papillae bulbous, less than two times as long as thick. ELC with 15 elements; ILC with 26. Insertion for ELC on tips of elements of ILC. ILC elements broad, with rounded tips; in palisade. Insertion for ILC at 1/4 or less of BC depth. Septum intracoronare origin on BC. Walls of BC concave; thicker anteriorly. Buccal cavity wider than deep. Dorsal gutter elongate, more than 1/2 depth of BC. Deirids and excretory pore 440–500 from anterior end.

Male. Body length 7.5–8.0 mm. Esophagus length 440–500. BC width 50–60, depth 18–20 dorsally and 24 ventrally. Spicule length 1.0–1.1 mm. Gubernaculum with large handle, ventral notch inconspicuous; length 156–161. Dorsal ray length 380. Ventral rays length equal to laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone paired, plates fused medially with numerous, long, sharp projections. Protrusions of dermal collar absent.

Female. Body length 7.5–8.0 mm. Esophagus length 380–451. BC width 40–68, depth 20–29. Vagina length 400–480. Anus to tail tip 120. Egg size 90–100 × 40–48. Infundibulum length about equal to sphincter length. Tail of mature female digitiform, straight, tip pointed; sublateral protrusions undeveloped.

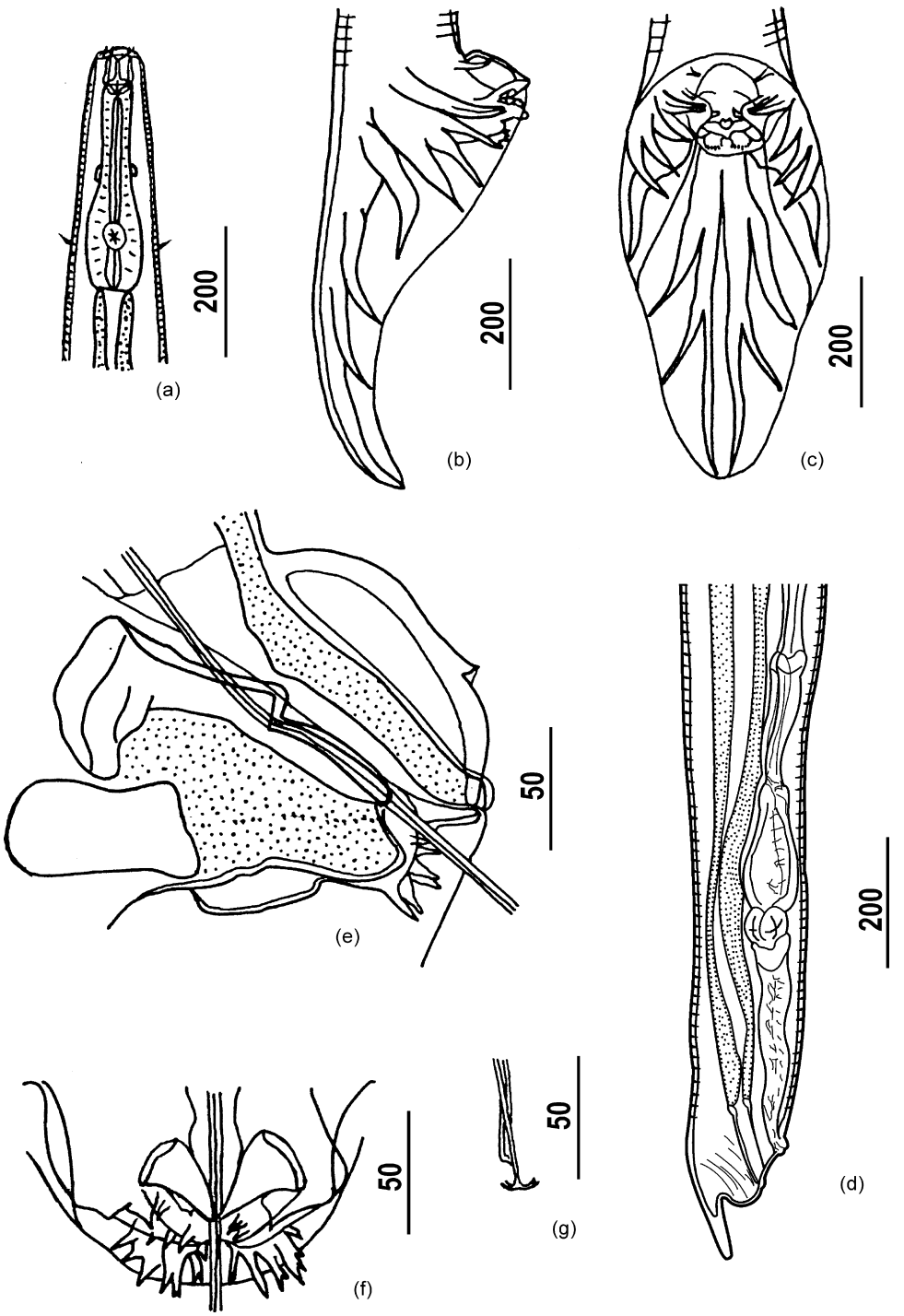

Fig. 47. *Cylicostephanus calicatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

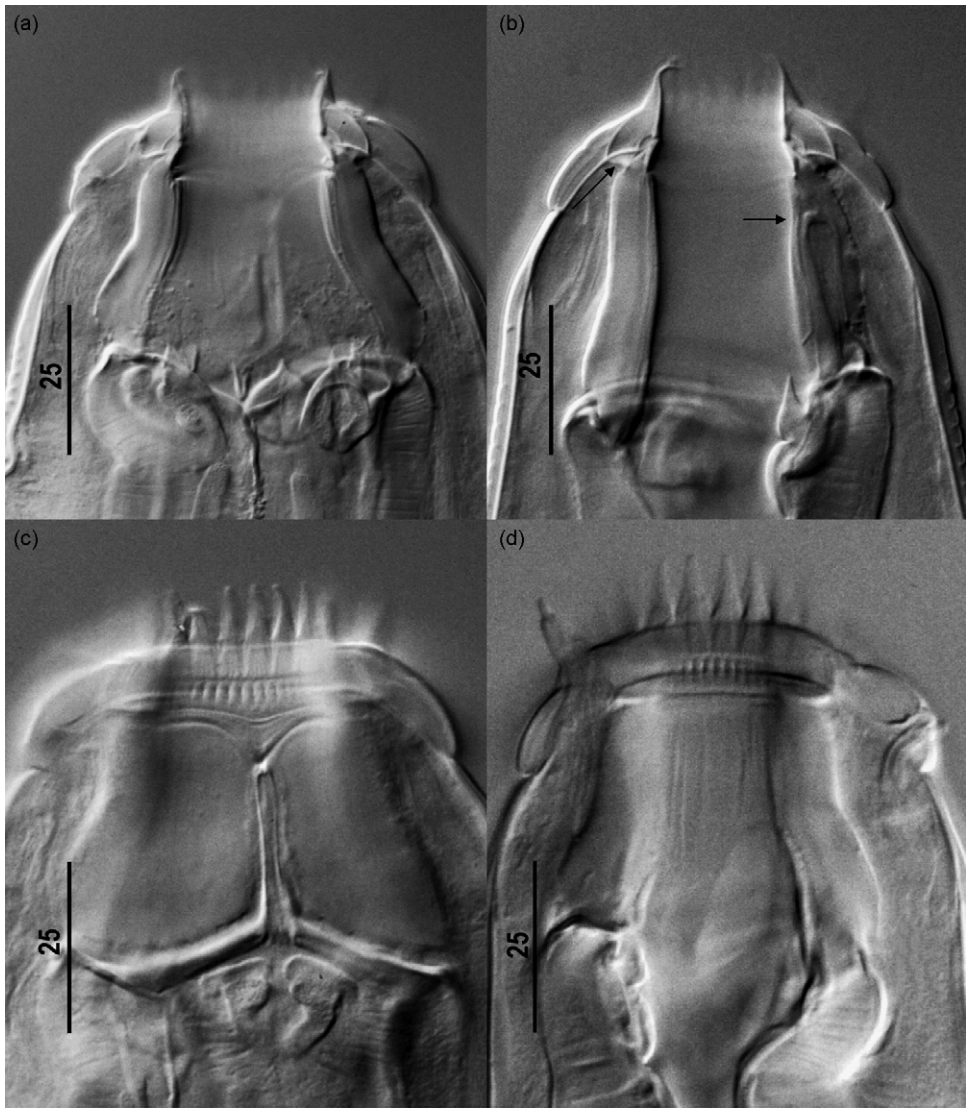

Fig. 48. *Cylicostephanus calicatus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing dorsal gutter (arrow) in wall of BC. (c) Dorsal gutter and elements of ILC and ELC, dorsal view. (d) Submedian papilla, elements of ILC and ELC and lateral papilla (on right side), subdorsal view.

Hosts. *Equus caballus*, *E. asinus*.
Locality. Cecum, colon.
Distribution. Cosmopolitan.

6.3.4. C. bidentatus (Ihle, 1925) Lichtenfels, 1975 (Figs. 51 and 52)

Synonyms. *Cylicostomum bidentatum* Ihle, 1925; *Cylicotetrapedon bidentatum* (Ihle, 1925) Ihle, 1925; *Trichonema bidentatum* (Ihle, 1925) Yorke and Maplestone, 1926; *Schulzitrichonema bidentatum* (Ihle, 1925) Baruš, 1963.

General. Tip of submedian papillae cone-shaped, two times as long as thick. ELC with 16 elements; ILC with 22. Elements of ELC triangular, longer than broad, tips pointed, insertion on tips of elements of ILC. Elements of ILC oval-shaped, longer than broad, tips rounded. Insertion for ILC at 1/4 or less of BC depth. Septum intracoronare origin on BC. Walls of BC straight, thicker anteriorly. Buccal cavity wider than deep. Dorsal gutter elongate, more than 1/2 depth of BC. Esophageal funnel enlarged; lined with exceptionally thick cuticle. Subventral esophageal teeth exceptionally large; protrude into buccal cavity. Deirids 210–229 from anterior end.

Male. Body length 5.7–7.5 mm. Esophagus length 410–530. BC width 60, depth 21 dorsally and 33

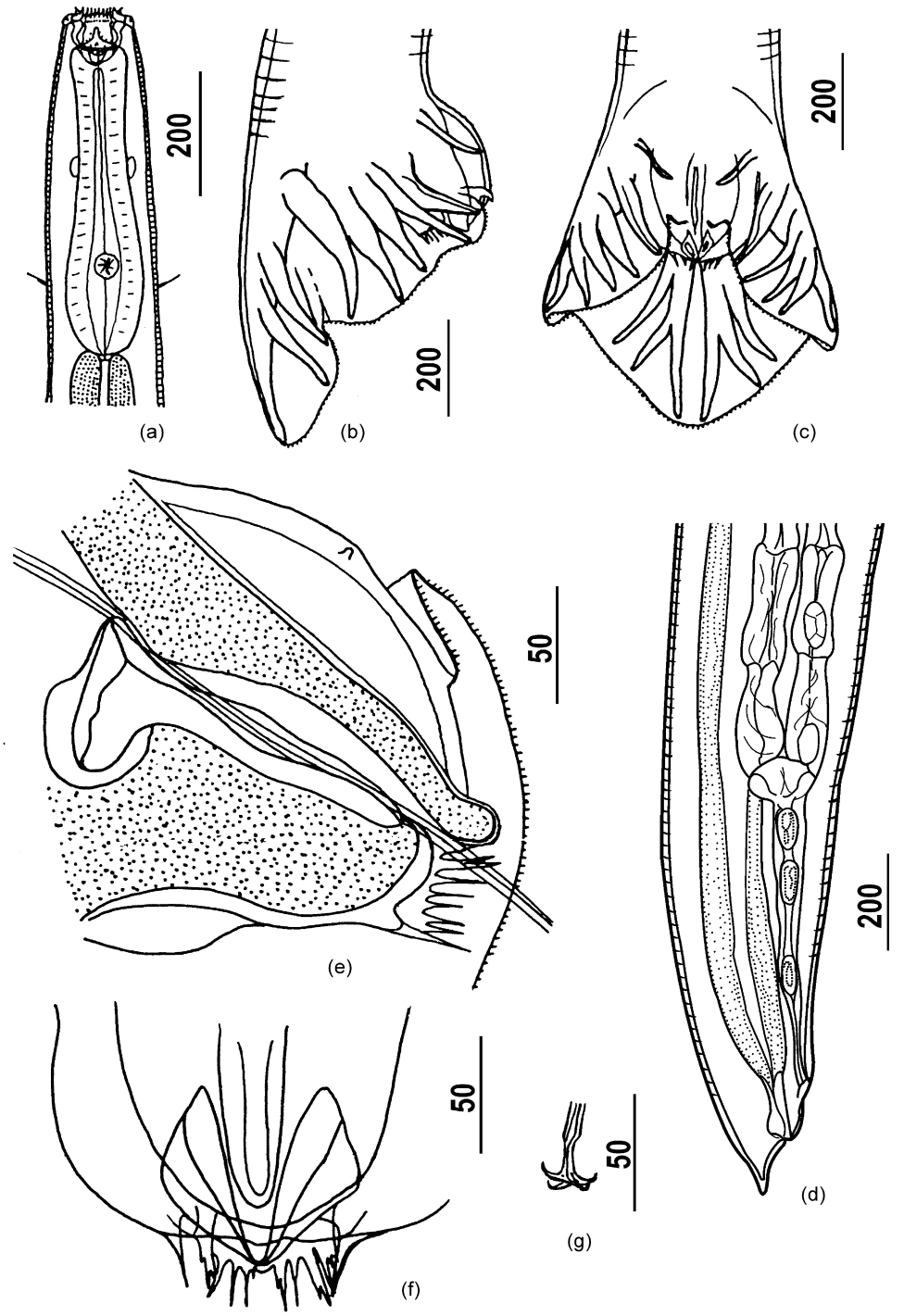

Fig. 49. *Cylicostephanus asymetricus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

ventrally. Spicule length 1.12 mm. Gubernaculum with large handle, ventral notch inconspicuous; length 180–192. Dorsal ray length 430. Ventral rays longer than laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone paired conical projections, with finger-shaped appendage on each. Paired, long, pointed protrusions of dermal collar present.

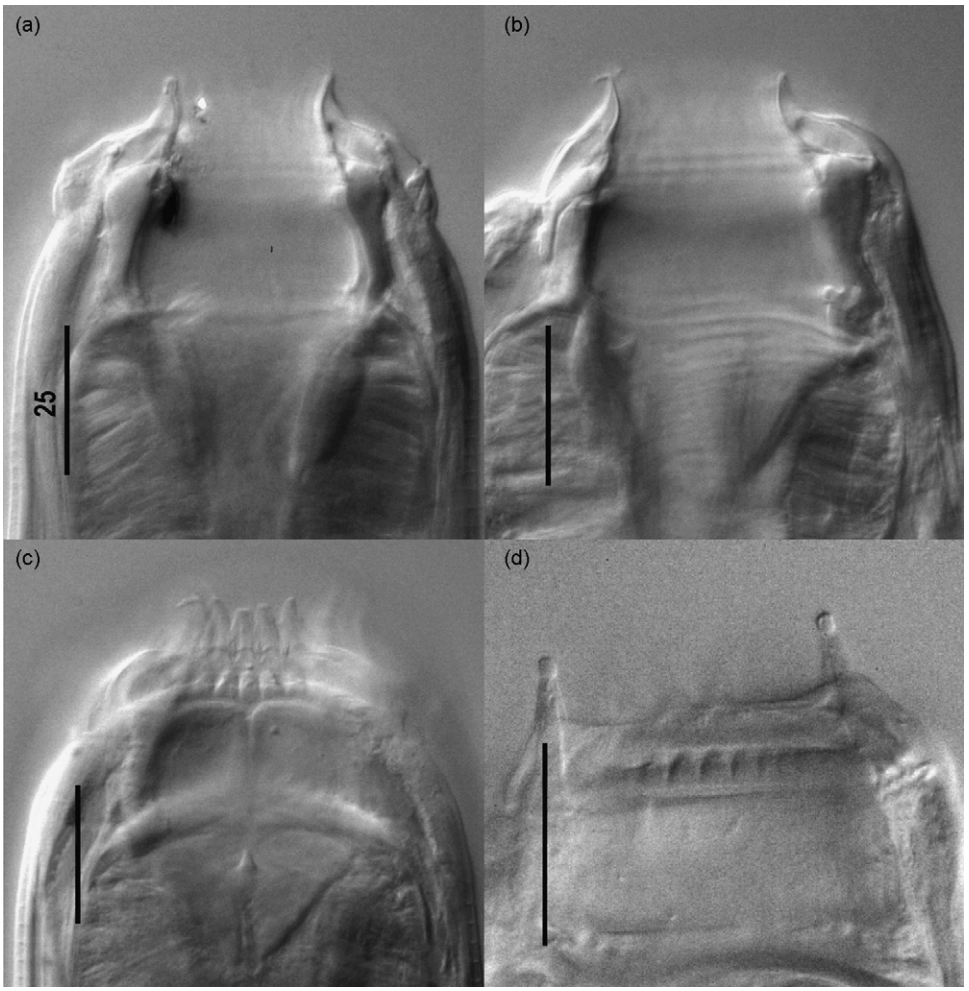

Fig. 50. *Cylicostephanus asymetricus*. (a) Buccal capsule, dorsoventral view, showing concave walls of BC. (b) Buccal capsule, lateral view, showing concave ventral wall of BC on right and dorsal gutter in wall of BC and dorsal esophageal tooth in esophageal funnel on left. (c) Elements of ILC and ELC, dorsal gutter and small, triangular dorsal esophageal tooth. (d) Submedian papillae with short, bulbous tips and elements of ILC.

Female. Body length 9.5 mm. Esophagus length 530. BC width 40–68, depth 20–29. Vulva to anus 145. Anus to tail tip 110. Egg size 95–105 × 44–48. Ovejector infundibulum length about equal to sphincter length. Tail of mature female digitiform, straight, tip pointed; sublateral protrusions undeveloped.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.3.5. *C. goldi (Boulenger, 1917) Lichtenfels, 1975 (Figs. 53 and 54)*

Synonyms. *Cylichnostomum goldi* Boulenger, 1917; *Cylicostomum goldi* (Boulenger, 1917) Ransom and Hadween, 1918; *Trichonema goldi* (Boulenger, 1917), Le Roux, 1924; *Cylicocercus goldi* (Boulenger, 1917) Cram, 1924; *Schulzitrichonema goldi* (Boulenger, 1917) Ershov, 1943; *Cylicotetrapedon goldi* (Boulenger, 1917) K'ung, 1964; *Cylicostomum tridentatum* Yorke and Macfie, 1920; *Cylicostomum ornatum* Kotlán, 1919; *Trichonema ornatum* (Kotlán, 1919) Le Roux, 1924; *Cylicostomias ornatum* (Kotlán, 1919) Cram, 1925; *Cyathostomum ornatum* (Kotlán, 1919) McIntosh, 1933; *Cylicodontophorus ornatum* (Kotlán, 1919) Ershov, 1939; *Cylicostephanus ornatus* (Kotlán, 1919) Lichtenfels, 1975.

General. Tip of submedian papillae cone-shaped, two times as long as thick. ELC with 20–22 elements; ILC with 30–38. Insertion for ELC on tips of elements of ILC. Tips of elements of ILC pointed, insertion at 1/4 or less of BC depth. Septum intracoronare origin placed on BC. Walls of BC with compound curve, thicker anteriorly. Buccal cavity wider than deep.

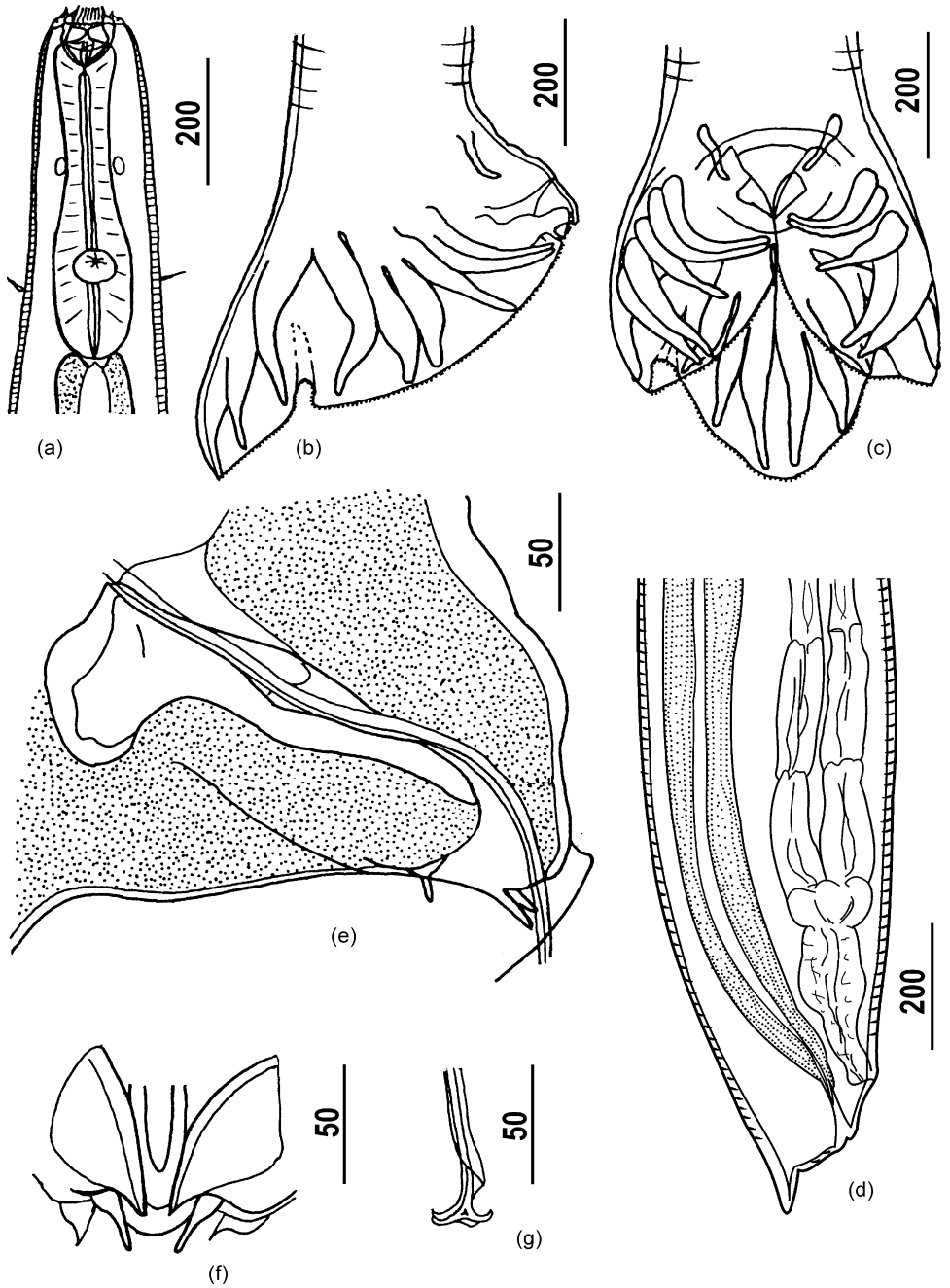

Fig. 51. *Cylicostephanus bidentatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

Dorsal gutter button-like. Deirids and excretory pore 250–300 from anterior end.

Male. Body length 5.2–7.8 mm. Esophagus length 200–422. BC width 48–65, depth 22–24. Spicule length 852–987. Gubernaculum large, with dorsal handle and ventral notch; length 156–189. Dorsal ray length 308–495. Ventral rays length equal to laterals. Genital cone conical, slightly protrudes beyond copulatory bursa. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone absent. Paired protrusions of dermal collar present.

Female. Body length 5.7–9.2 mm. Esophagus length 408–500. BC width 52–78, depth 24–26. Vulva to tail tip 178–212. Anus to tail tip 86–110. Egg size

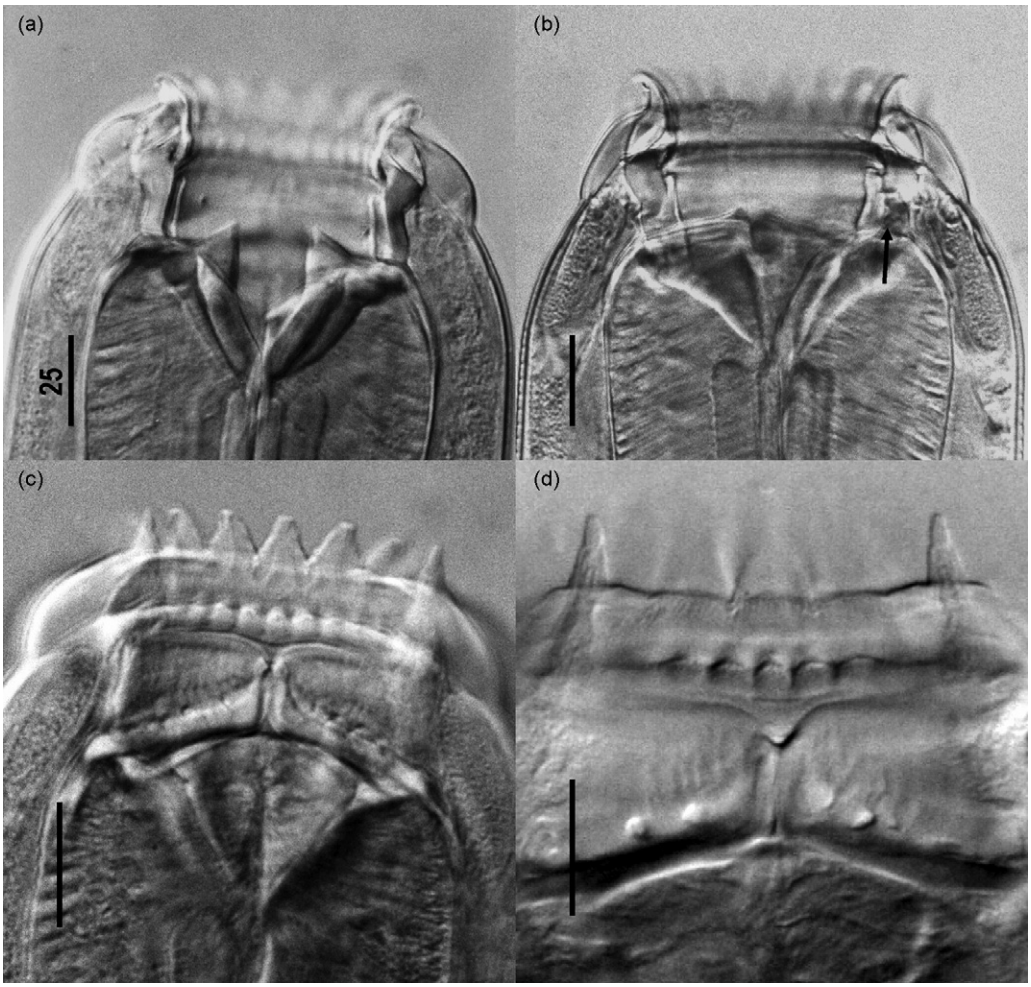

Fig. 52. *Cylicostephanus bidentatus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing thick dorsal gutter (arrow) in wall of BC. (c) Submedian papillae with cone-shaped tips, elements of ILC and ELC and dorsal gutter. (d) Submedian papillae, elements of ILC and ELC and dorsal gutter.

100–114 × 47–56. Ovejector infundibulum length about equal to sphincter length. Tail of adult females digitiform, curved dorsally at right angle; sublateral and ventral protrusions well-developed.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.3.6. *C. hybridus (Kotlán, 1920) Cram, 1924 (Figs. 55 and 56)*

Synonyms. *Cylicostomum hybridum* Kotlán, 1920; *Trichonema hybridum* (Kotlán, 1920) Le Roux, 1924; *Erschowinema hybridum* (Kotlán, 1920) Tschoijo, 1957; *Schulzitrichonema hybridum* (Kotlán, 1920) Baruš, 1963.

General. Tip of submedian papillae spindle-shaped, three to four times as long as thick. ELC with 14–16 elements; ILC with 30–34. Insertion for ELC on tips of elements of ILC. Tips of elements of ILC rounded. Insertion for ILC on anterior edge of BC. Septum intracoronare origin placed on support. BC walls straight, thicker posteriorly. Buccal cavity about as wide as deep. Dorsal gutter elongate, more than $^1/_2$ depth of BC. Deirids and excretory pore 330–430 from anterior end.

Male. Body length 6.6–8.5 mm. Esophagus length 320–412. BC width 36–40, depth 24–32. Spicule length 1.04–1.12 mm. Gubernaculum large, with dorsal handle & ventral notch; length 152–172. Dorsal ray length 260–358. Ventral rays shorter than laterals. Dermal collar well-developed on ventral side of genital cone.

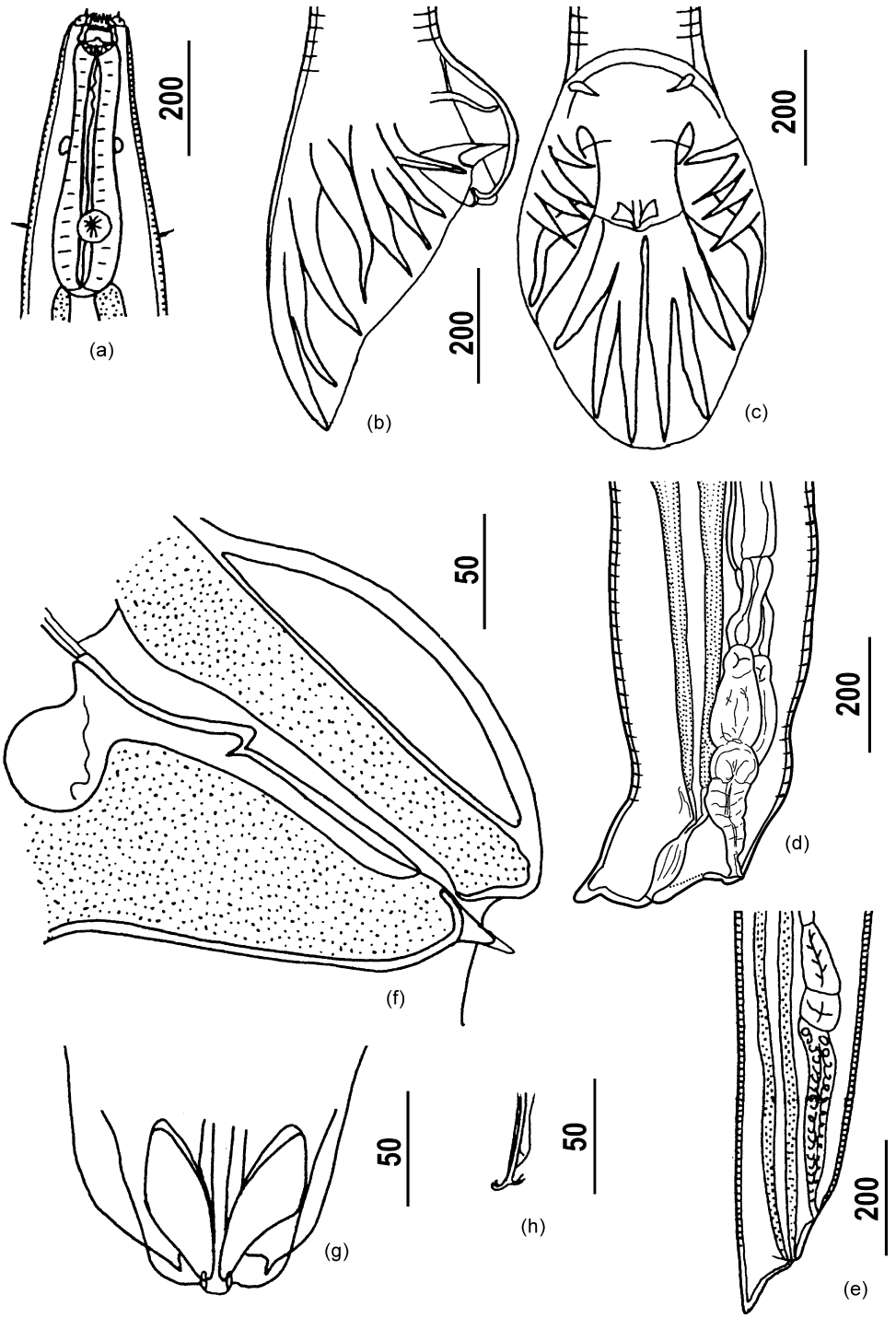

Fig. 53. *Cylicostephanus goldi*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. d, (e) Tails of females, showing variations that may be due to maturity of specimen. (f) Genital cone, lateral view. (e) Tip of genital cone, ventral view. (h) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

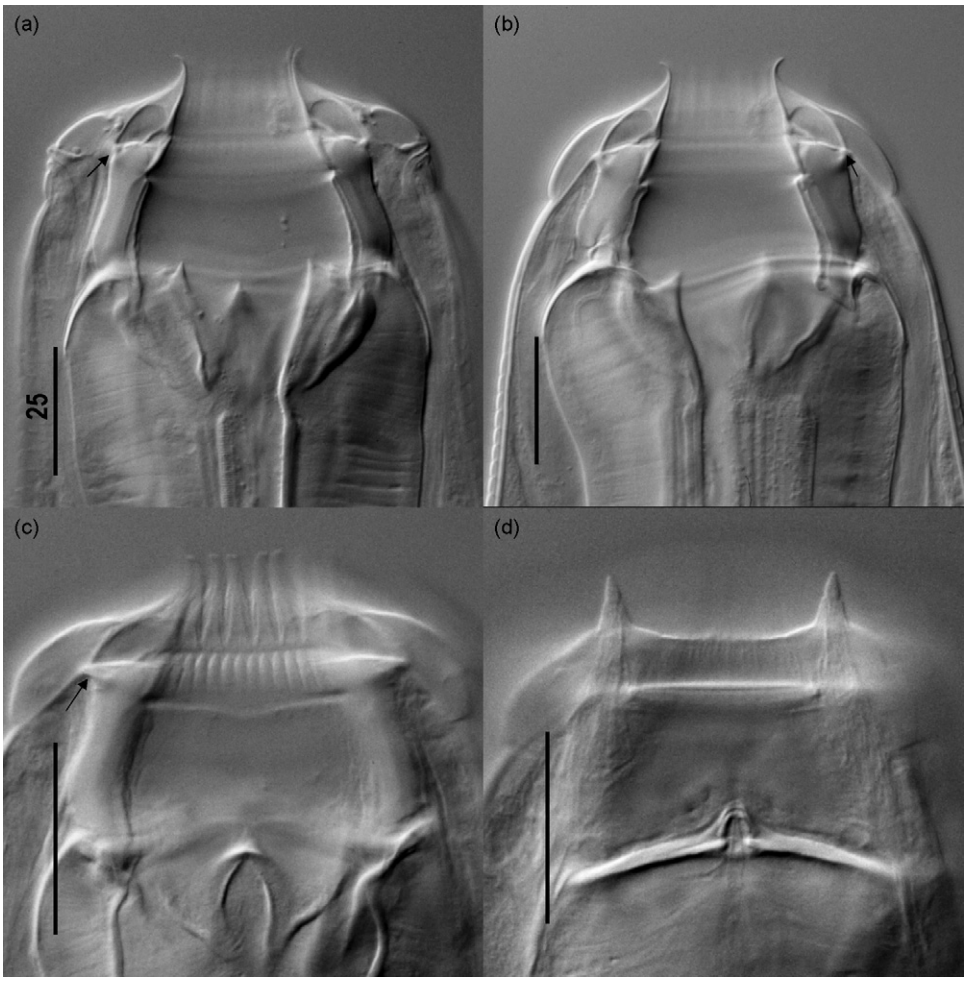

Fig. 54. *Cylicostephanus goldi*. (a) Buccal capsule, dorsoventral view, showing small triangular support for ELC. (b) Buccal capsule, lateral view, showing short dorsal gutter in wall of BC at left. (c) Elements of ILC and ELC, dorsal view, showing triangular support for ELC. (d) Submedian papillae with cone-shaped tips and dorsal gutter.

Appendages of genital cone paired, ovoid-shaped bodies connected medially, without any projections. Protrusions of dermal collar absent.

Female. Body length 8.2–9.2 mm. Esophagus length 400–475. BC width 28–32, depth 28–32. Vulva to tail tip 180–200. Anus to tail tip 94–116. Egg size 88–96 × 47–50. Ovejector infundibulum longer than sphincter. Tail conical; sublateral protrusions poorly developed.

Hosts. *Equus caballus*, *E. asinus*, *E. przewalskii*.

Locality. Cecum, colon.

Distribution. Asia, Europe, North America.

6.3.7. *C. longibursatus* (Yorke and Macfie, 1918) Cram, 1924 (Figs. 57 and 58)

Synonyms. *Cylicostomum longibursatum* Yorke and Macfie, 1918; *Trichonema longibursatum* (Yorke and Macfie, 1918) Le Roux, 1924; *Cylicostomum nanum* Ihle, 1919; *Cylicostomum calicatiforme* Kotlán, 1919.

General. Tips of submedian papillae cone-shaped, two to three times as long as thick. ELC has same number elements (14–18) as ILC. Insertion for ELC slightly back from tips of elements of ILC. Tips of elements of ILC pointed. Insertion point for posterior ends of elements of ILC at 1/4 or less of BC depth. Septum intracoronare origin on BC. Walls BC with compound curve, thicker anteriorly. Buccal cavity wider than deep. Dorsal gutter button-like. Deirids and excretory pore 272–287 and 243–258 from anterior end.

Male. Body length 4.3–6.9 mm. Esophagus length 252–306. BC width 28–32, depth 16–22. Spicule length 548–977. Gubernaculum large, with dorsal handle and ventral notch; length 132–148. Dorsal ray length 594–800. Ventral rays shorter than laterals. Dermal collar

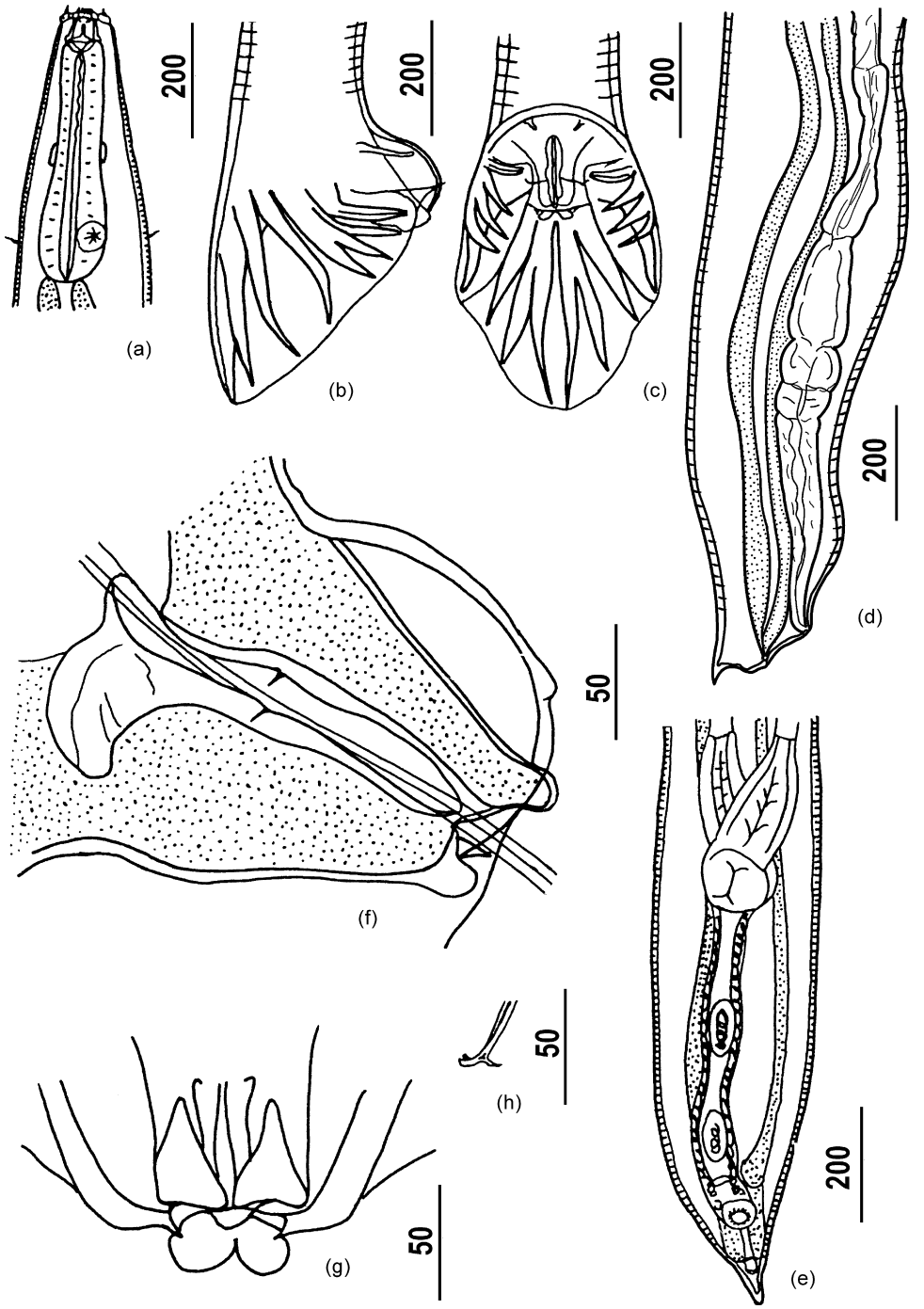

Fig. 55. *Cylicostephanus hybridus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female, lateral view. (e) Tail of female, ventral view. (f) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (h) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

well-developed on ventral side of genital cone. Appendages of genital cone paired, massive oval formations, fused medially, with numerous short projections on ventral side.

Female. Body length 4.7–8.0 mm. Esophagus length 256–340. BC width 26–33, depth 20–26. Vulva to tail tip 127–216. Anus to tail tip 95–130. Egg size 85–93 × 40–46. Ovejector infundibulum length about

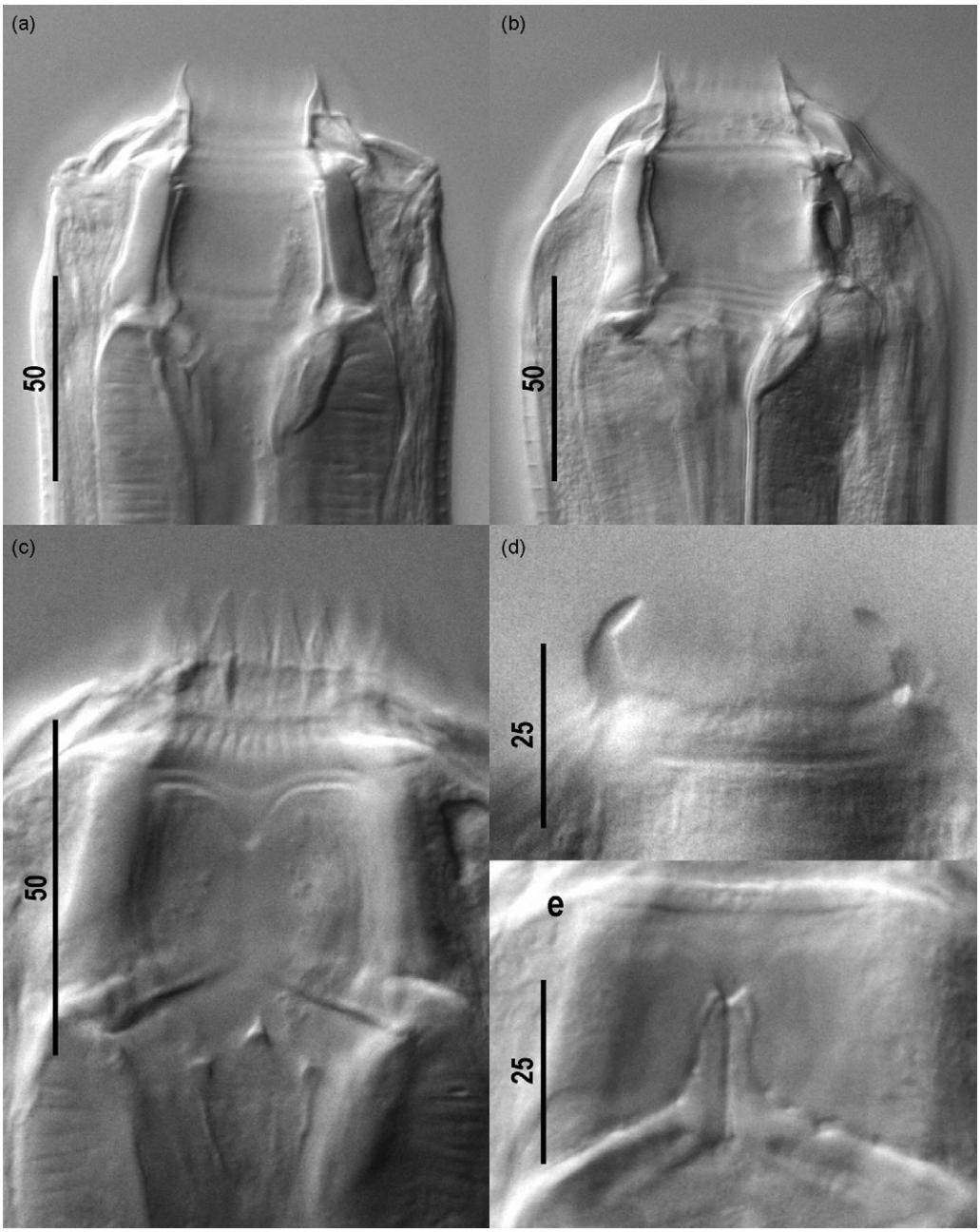

Fig. 56. *Cylicostephanus hybridus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Elements of ILC and ELC, dorsal view. (d) Submedian papillae. (e) Dorsal gutter, dorsal view.

equal to sphincter length. Tail of mature females digitiform, straight, tip pointed; sublateral protrusions poorly developed.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.3.8. C. minutus (Yorke and Macfie, 1918) Cram, 1924 (Figs. 59 and 60)

Synonyms. *Cylicostomum minutum* Yorke and Macfie, 1918; *Trichonema minutum* (Yorke and Macfie, 1918) Le Roux, 1924; *Erschowinema minutum* (Yorke and Macfie, 1918) Tschoijo, 1957 *Cylicostomum calicatum* var. *minus* Kotlán, 1920.

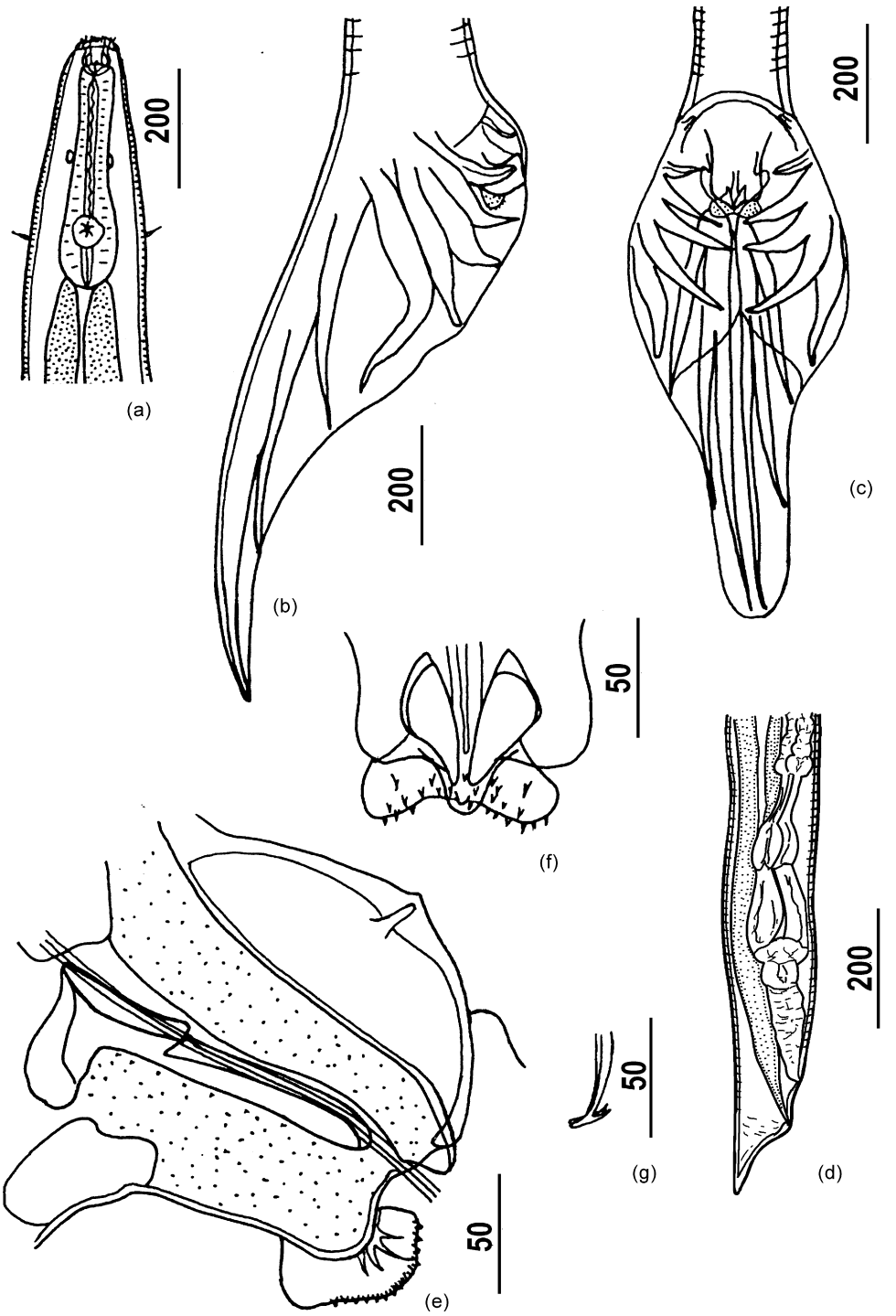

Fig. 57. *Cylicostephanus longibursatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

General. Tip of submedian papillae spindle-shaped, two to three times as long as thick. ELC with 8 elements; ILC with 18–22. Insertion for ELC on tips of elements of ILC. Tips of elements of ILC rounded. Insertion for ILC on anterior edge of BC. Septum intracoronare origin on support. Walls of BC straight, thicker posteriorly. Buccal cavity deeper than wide. Dorsal gutter elongate, more than $^1/_2$ depth of BC.

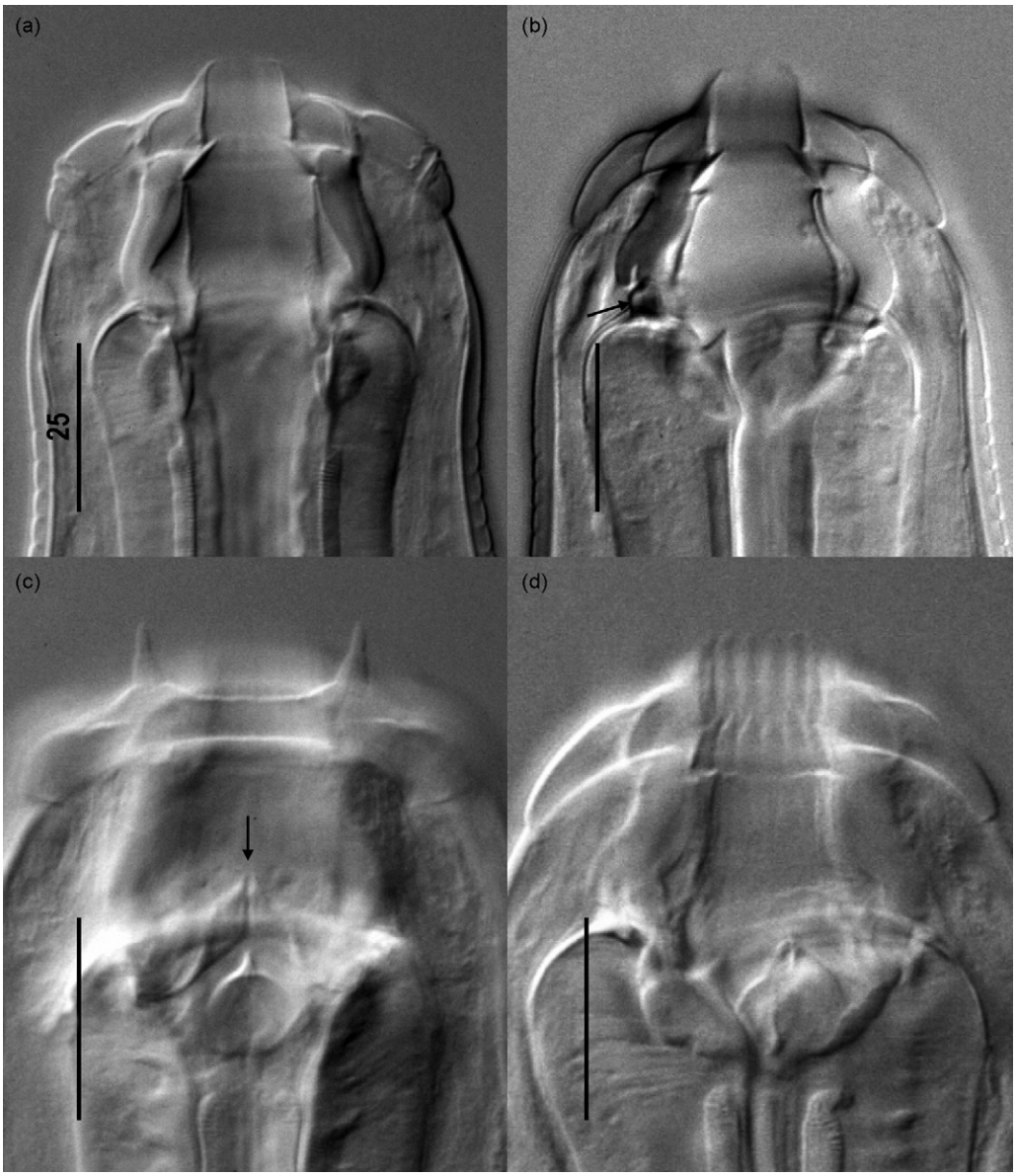

Fig. 58. *Cylicostephanus longibursatus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing short dorsal gutter (arrow) in wall of BC and small dorsal tooth. (c) Submedian papillae, dorsal gutter (arrow) and dorsal tooth (d) Elements of ILC and ELC, lateral view.

Male. Body length 4.0–5.2 mm. Esophagus length 270–388. BC width 18–24, depth 24–27. Spicule length 515–672. Gubernaculum large, with dorsal handle and ventral notch; length 92–110. Dorsal ray length 140–170. Ventral and lateral rays of equal length. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone paired, long, finger-shaped, bifurcated distally, proximally fused in semispherical mass.

Female. Body length 4.6–6.8 mm. Esophagus length 284–382. BC width 22–28, depth 26–30. Vulva to tail tip 100–187. Anus to tail tip 54–120. Egg size 53–60 × 34–37. Tail conical. Ovejector infundibulum longer than sphincter.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.3.9. Discussion

The name *Cylicostephanus* was coined by Ihle (1922) as a subgenus to draw attention to the depressed

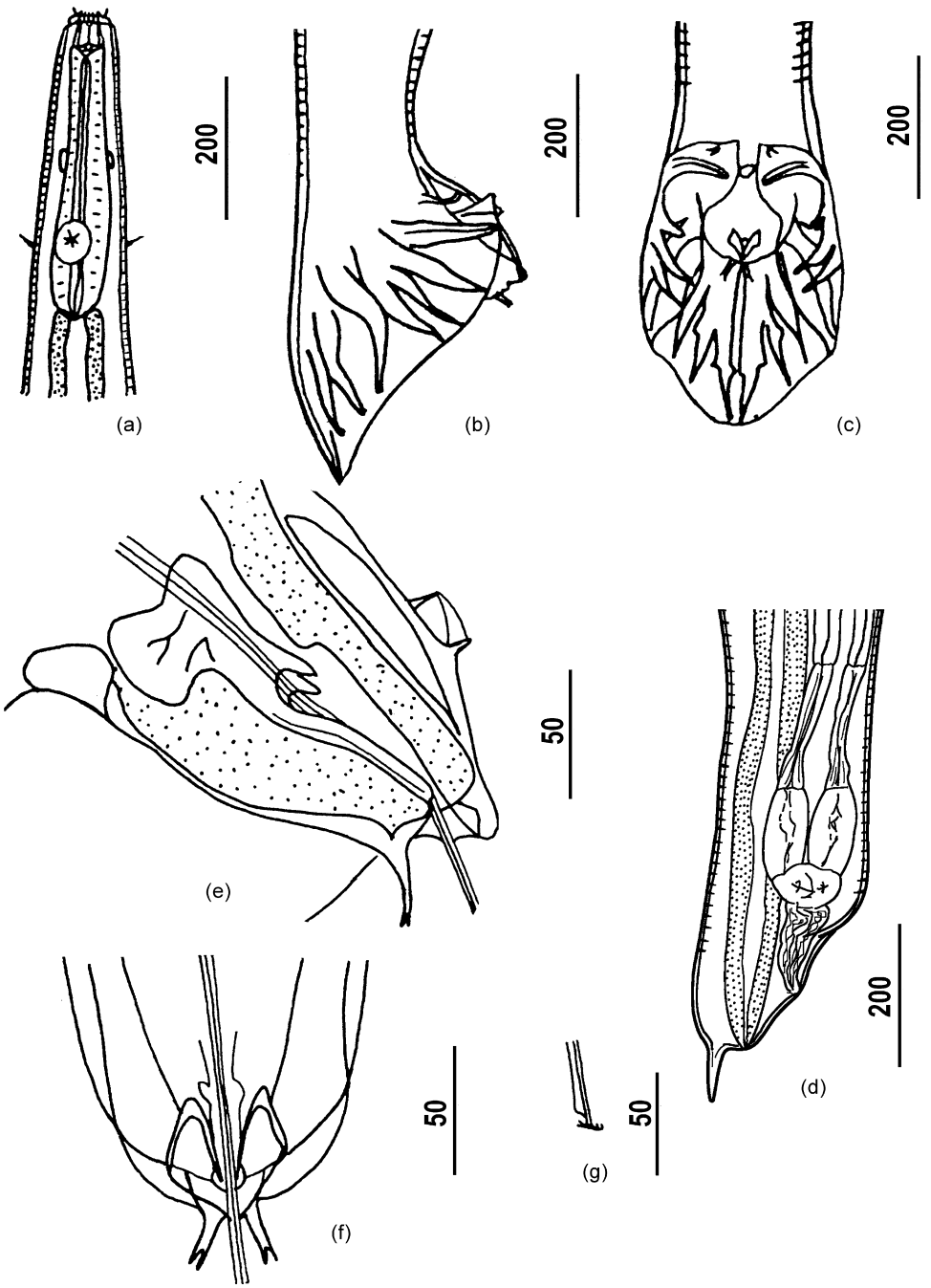

Fig. 59. *Cylicostephanus minutus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

mouth collar of a group of species including *C. calicatus*, *C. longibursatus*, *C. minutus*, *C. hybridus*, and *C. poculatus* These species also share the characteristics of an ILC composed of short rods implanted close to the anterior edge of the buccal capsule; an ELC composed of longer and broader elements; and a buccal cavity that is slightly narrower anteriorly than posteriorly. Most subsequent workers have grouped these five species together. To this group Cram (1925) added the species *C. asymetricus*. *Cylicostephanus bidentatus*, a species considered by some workers to be a synonym of *C. asymetricus*, is

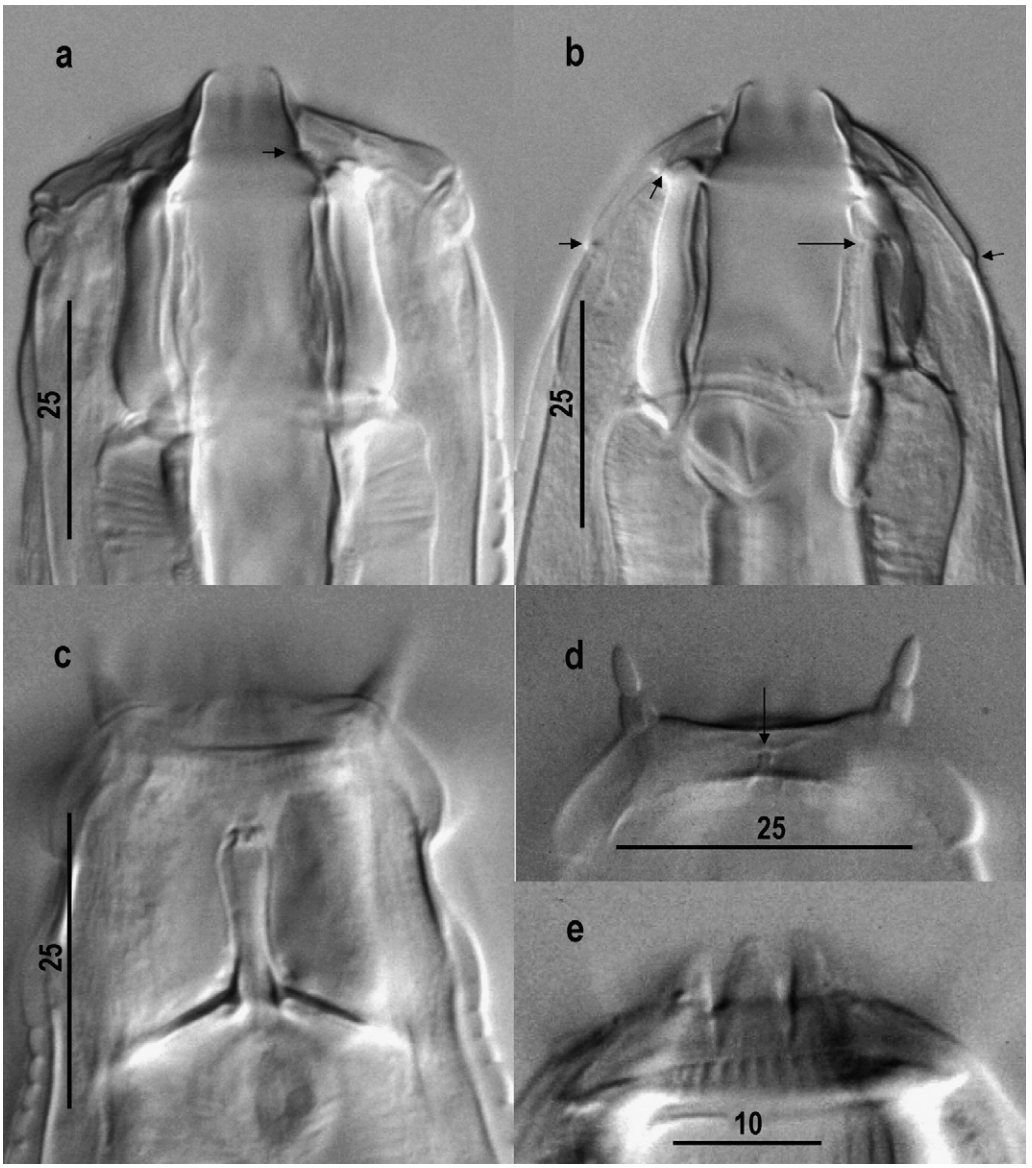

Fig. 60. *Cylicostephanus minutus*. (a) Buccal capsule, dorsoventral view. Arrow marks junction of ELC and ILC. (b) Buccal capsule, lateral view, showing small triangular support (uppermost arrow), posterior limit of mouth collar (outer arrows) and orifice (medial arrow) of dorsal gutter in wall of BC. (c) Dorsal gutter, dorsal view. (d) Submedian papillae and lateral papilla (arrow), lateral view. (e) Elements of ELC and ILC.

recognized as a separate species because of its large esophageal teeth and relative lack of asymmetry of the buccal capsule.

The common species, *C. goldi*, fits well the characteristics of this genus, being very similar in cephalic characteristics to *C. longibursatus*, and was included by Lichtenfels (1975) in *Cylicostephanus*.

Hartwich (1986) compared published descriptions of the two species and concluded that the description of the rarely reported and often misidentified *C. ornatum* is indistinguishable from *C. goldi*. Although there are several reports of *C. ornatum* in North America, all specimens that Lichtenfels (1975) could locate were redetermined as other species. We consider *C. ornatum* to be a synonym of *C. goldi*.

Trichonema parvibursatum has previously been considered to be a synonym of *C. hybridus*, but Hartwich (1986) discovered that the original description of this species more closely matches that of *C. goldi*.

Trichonema tsengi, described in China (K'ung and Yang, 1963), is considered to be a synonym of *C. calicatus*. It was separated from *C. calicatus* by

a greater number and differently shaped ELC elements. As Baruš (1962) and Braide and Georgi (1974) have shown, however, *C. calicatus* has a greater range in number of ELC elements (12–18) than given in earlier reports.

Cylicotetrapedon was recognized at the level of genus by Dvojnos and Kharchenko (1994) following several earlier workers who all recognized the same two species in this group. However, neither Lichtenfels (1975) nor Hartwich (1986) could find characters without considerable homoplasy to define this group. The consensus of the 1997 Sun City Workshop (Lichtenfels et al., 1998) was that *Cylicotetrapedon* not be used.

6.4. *Skrjabinodentus* Tshoijo in Popova (1958)

General. Small-sized Cyathostominea. MC flattened, divided into inner and outer rings. Posterior edge of MC posterior to anterior edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae spindle-shaped, two to three times or more as long as thick. Stalk of submedian papillae broader than long. ELC and ILC elements of similar length; ELC elements markedly less numerous or nearly equal in number to ILC. Elements of ELC longer than broad or as long as broad, tips pointed; insertion point on tips of ILC. Elements of ILC as long as broad or broader than long, tips pointed or rounded; insertion point at 1/4 or less of BC depth. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, short, triangular in optical section. Septum intracoronare origin on support. Medial insertion of septum intracoronare anterior to junction of ELC and ILC. Walls of BC S-shaped, much thicker anteriorly. Buccal cavity wider than deep, wider posteriorly. Dorsal gutter well-developed, 1/3–2/3 of depth of BC. Buccal teeth absent. Esophageal funnel enlarged, lined with thick cuticle. Esophageal teeth prominent. Anterior muscular portion of esophagus about 1/4–1/3 of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus or near EI.

Male. Proximal and middle rays of dorsal ray fused. Ventral rays may have different length relative to laterals. Dorsal lobe longer then lateral lobes. Externodorsal rays origin at junction of dorsal and laterals rays. Gubernaculum large, small handle, enlarged distal tip. Genital cone elongate, extends beyond bursal edge. Spicule tips hook- or harpoon-shaped.

Female. Vulva more than one tail length from anus. Vagina longer than sphincter. Ovejector vestibule oval or Y-shaped; infundibulum longer than sphincter. Tail conical or digitiform, short, length less than 2× diameter at anus.

Type species. *S. caragandicus* (Funikova, 1939) Tshoijo in Popova (1958).

6.4.1. Key to species of *Skrjabinodentus*

(1) a. ELC with 13–16 or more elements	*S. longiconus*
b. ELC with eight elements	2
(2) a. ILC with eight elements	*S. tshoijoi*
b. ILC with 16–18 elements	*S. caragandicus*

6.4.2. *S. caragandicus* (Funikova, 1939) Tshoijo in Popova (1958) (Figs. 61 and 62)

Synonyms. *Trichonema caragandicum* Funikova, 1939; *Cylicostephanus caragandicus* Hartwich, 1986.

General. Elements of ELC markedly less numerous (8) than ILC (16–18); and longer than ILC. Elements of ILC longer than broad. Elements of ELC as long as broad. Tips of elements of ILC rounded. ILC insertion point less than 1/4 of BC depth. Excretory pore and deirids near EI.

Male. Body length 8.0–10.0 mm. Esophagus length 303–332. BC width 46–58, depth 17–25. Spicule length 1.0–1.1 mm. Gubernaculum length 183–208. Dorsal ray length 428–571. Ventral rays shorter than laterals. Tip of external branch of dorsal ray bifurcated. Genital cone elongate cylindrical, extends beyond bursal edge. Dermal collar undeveloped. Appendages of genital cone paired, pointed rods fused proximally. Protrusions of dermal collar absent.

Female. Body length 8.0–12.6 mm. Esophagus length 340–347. BC width 50–54, depth 17–25. Vagina length 291. Vulva to tail tip 374–415. Anus to tail tip 129–158. Egg size 97–108 × 47–53. Tail of mature females straight, tip sharply pointed.

Hosts. *Equus caballus*, *E. caballus* × *E. asinus*.

Locality. Cecum, colon.

Distribution. Asia.

6.4.3. *S. longiconus* (Scialdo-Krecek, 1983) Lichtenfels and Klei, 1988 (Figs. 63 and 64)

Synonyms. *Cylicostephanus longiconus* Scialdo-Krecek, 1983.

General. Elements of ELC markedly less numerous (13–16) than ILC (19–23); and longer than ILC. Elements of ELC longer than broad. Elements of ILC nearly as long as broad. Tips of elements of ILC rounded.

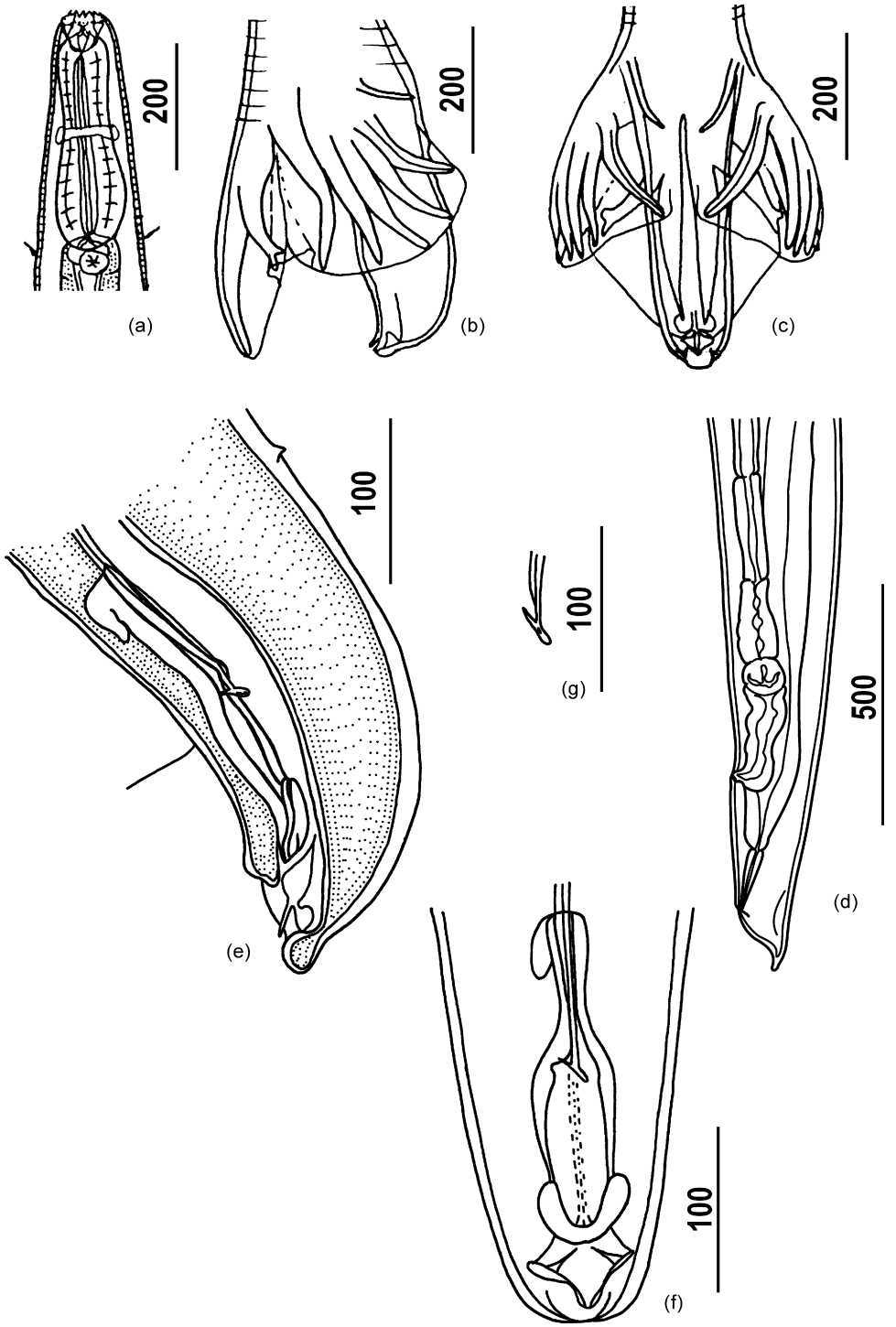

Fig. 61. *Skrjabinodentus caragandicus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

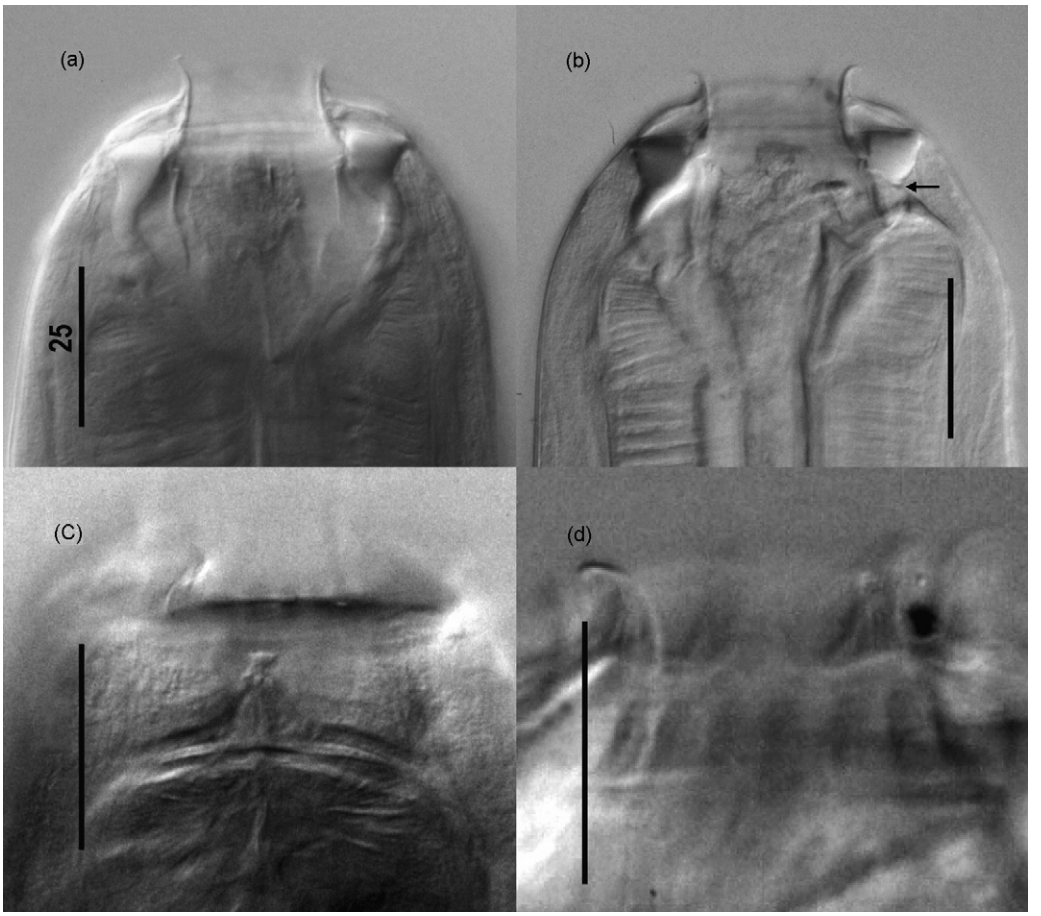

Fig. 62. *Skrjabinodentus caragandicus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view; dorsal tooth in esophageal funnel and dorsal gutter (arrow) in wall of BC. (c) Dorsal view of dorsal gutter. (d) Elements of ELC and ILC.

Insertion point of ILC less than 1/4 of BC depth. Excretory pore and deirids near middle of glandular esophagus, 380–411 from anterior end.

Male. Body length 8.2–10.4 mm. Esophagus length 396–507. BC width 42–50, depth 18–21. Spicule length 0.99–1.26 mm. Gubernaculum length 274–292. Dorsal ray length 435–448. Ventral rays shorter than laterals. Tip of external branch of dorsal ray bifurcated. Genital cone elongate, cylindrical, extends beyond bursal edge. Dermal collar undeveloped. Appendages of genital cone with paired, pointed rods fused proximally. Protrusions of dermal collar absent.

Female. Body length 8.2–12.6 mm. Esophagus length 486–628. BC width 43–62, depth 18–28. Vulva to tail tip 214–378. Anus to tail tip 107–198. Egg size 107–128 × 42–64.

Hosts. *Equus zebra hartmannae*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. South Africa.

6.4.4. S. tshoijoi Dvojnos and Kharchenko, 1986 (Figs. 65 and 66)

General. Both ELC and ILC consist of eight broader-than-long elements; tips of both pointed. Insertion point for posterior ends of elements of ILC about 1/3 of BC depth. Excretory pore and deirids near middle of glandular esophagus.

Male. Body length 7.8–9.1 mm. Esophagus length 442–476. BC width 60–68, depth 33–42. Distance from deirids to head end 347–414; from excretory pore 342–420. Spicule length 1.19–1.25. Gubernaculum length 228–255. Dorsal ray length 291–358. Ventral rays shorter than laterals. Tip of external branch of dorsal ray not bifurcated. Genital cone elongate, conical, extends beyond bursal edge. Dermal collar undeveloped. Appendages of genital cone with paired pointed rods fused proximally. Protrusions of dermal collar absent.

Female. Body length 8.0–9.8 mm. Esophagus length 498–510. BC width 60–68, depth 36–44. Distance from

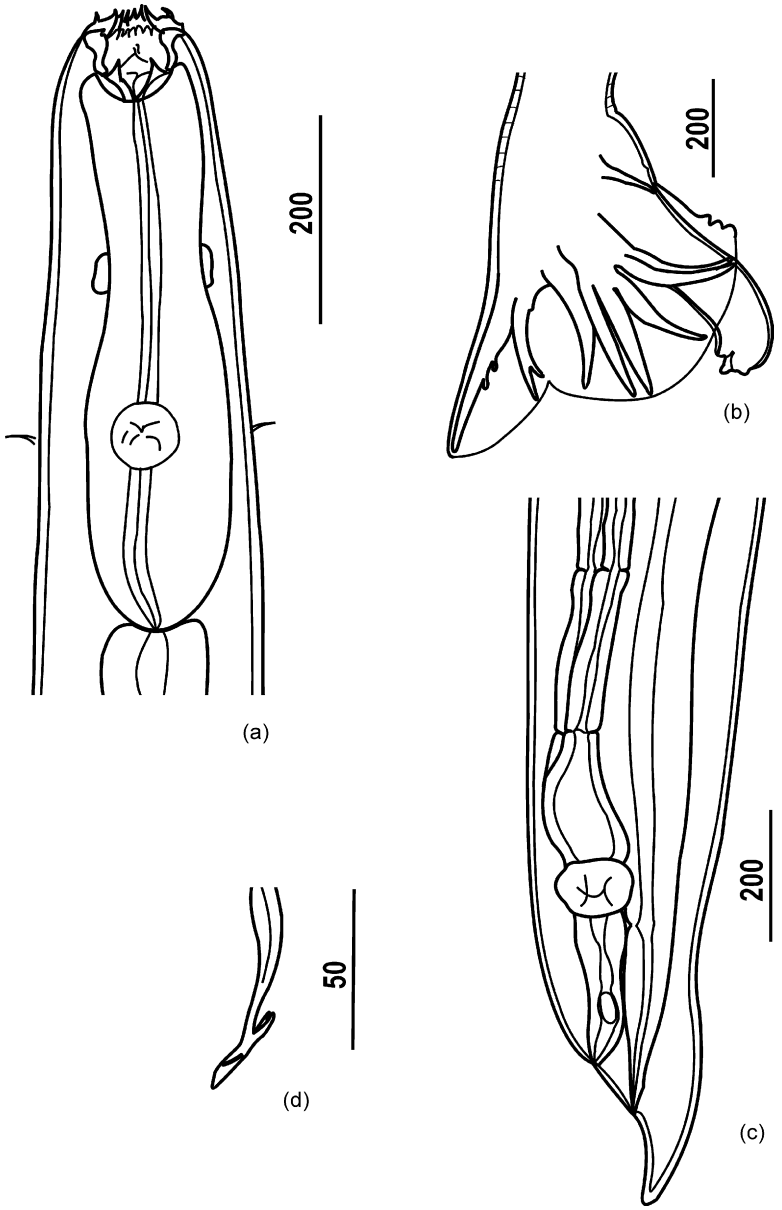

Fig. 63. *Skrjabinodentus longiconus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Tail of female. (d) Fused spicule tips of male.

deirids to head end 370–386, from excretory pore 370–392. Vulva to tail tip 342–420. Anus to tail tip 123–140. Eggs size 105–114 × 52–56.

Hosts. *Equus caballus*.

Locality. Cecum, colon.

Distribution. Asia.

6.4.5. Discussion

The three species in the genus *Skrjabinodentus* share several distinguishing characteristics: (1) the proximal and middle branches of the dorsal bursal ray are fused completely or almost to the distal tips; (2) the genital cone is greatly elongated and (3) the gubernaculum is modified by a reduction in size of the handle and the presence of posterior alae. Dvojnos and Kharchenko (1994) recognized *Skrjabinodentus* at genus level. Lichtenfels and Klei (1988) recommended the use of *Skrjabinodentus* at subgenus level within *Cylicostephanus*; and, Hartwich (1986) tentatively placed *C. caragandicus* in *Cylicostephanus*. The consensus of the 1997 Sun City Workshop (Lichtenfels et al., 1998) was to recognize this group of 3 similar species at genus level. Information is needed on the characteristics of the mouth collar and support for the ELC as described by

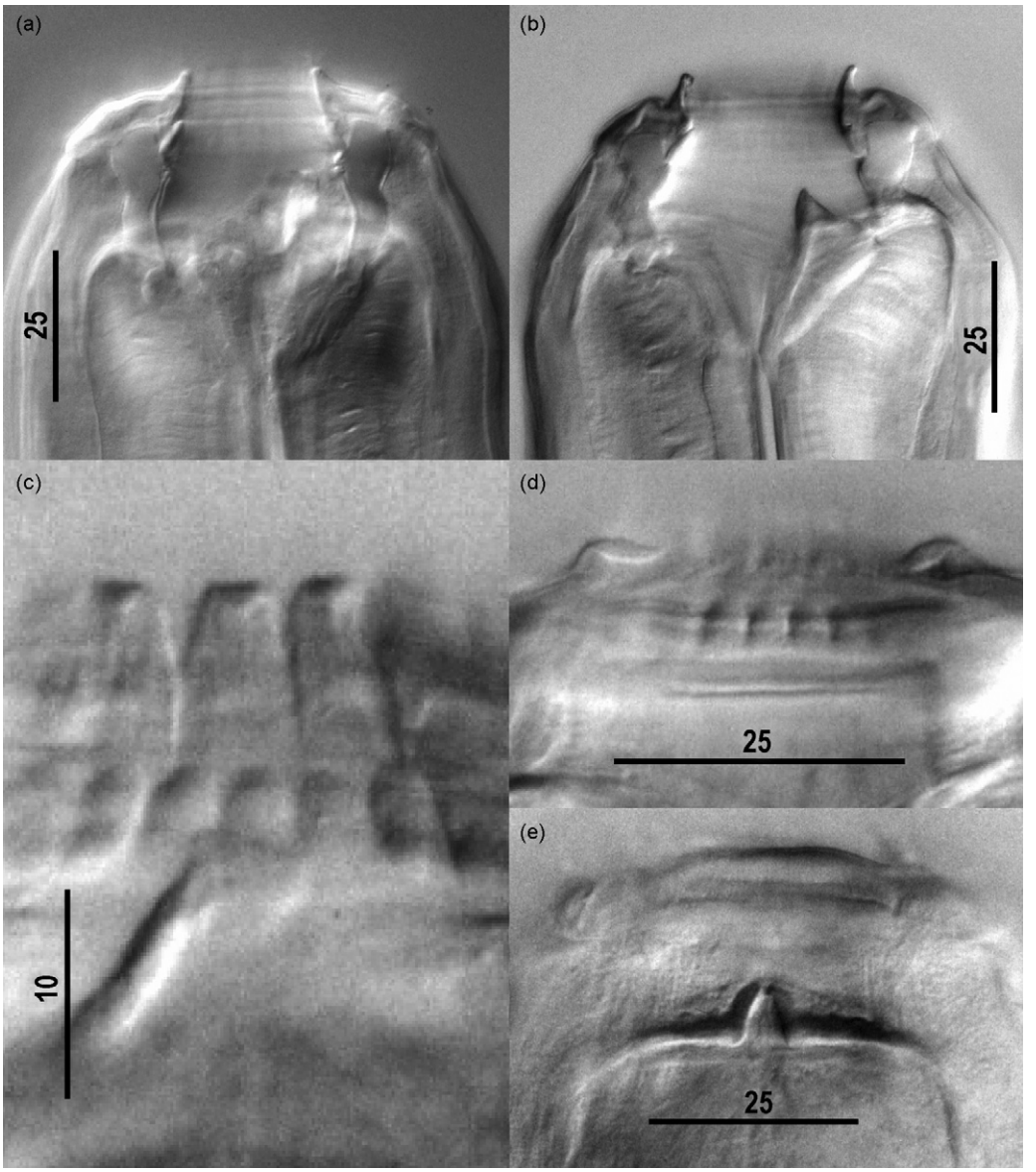

Fig. 64. *Skrjabinodentus longiconus.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing dorsal esophageal tooth. (c) Elements of ELC and ILC. (d) Submedian papillae and elements of ILC. (e) Dorsal gutter.

Hartwich (1986), and molecular studies are lacking. We prefer to continue to recognize this morphologically distinguished group of three species in *Skrjabinodentus* until molecular studies can determine whether they are separate from other groups of species now included within the genus *Cylicostephanus*.

6.5. *Cylicodontophorus* Ihle, 1922

Synonyms. *Cylicostomum* (*Cylicodontophorus*) Ihle, 1922.

General. Small to medium-sized Cyathostominea. MC inflated, high, ring-shaped, divided into inner and outer rings. Posterior edge of MC posterior or anterior to edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae bullet-shaped. Stalk of submedian papillae broader than long. Elements of ELC nearly equal in number to ILC and longer or equal in length to them. Elements of ELC longer than broad, tips pointed; insertion point on tips of ILC. Elements of ILC longer than broad, tips pointed or

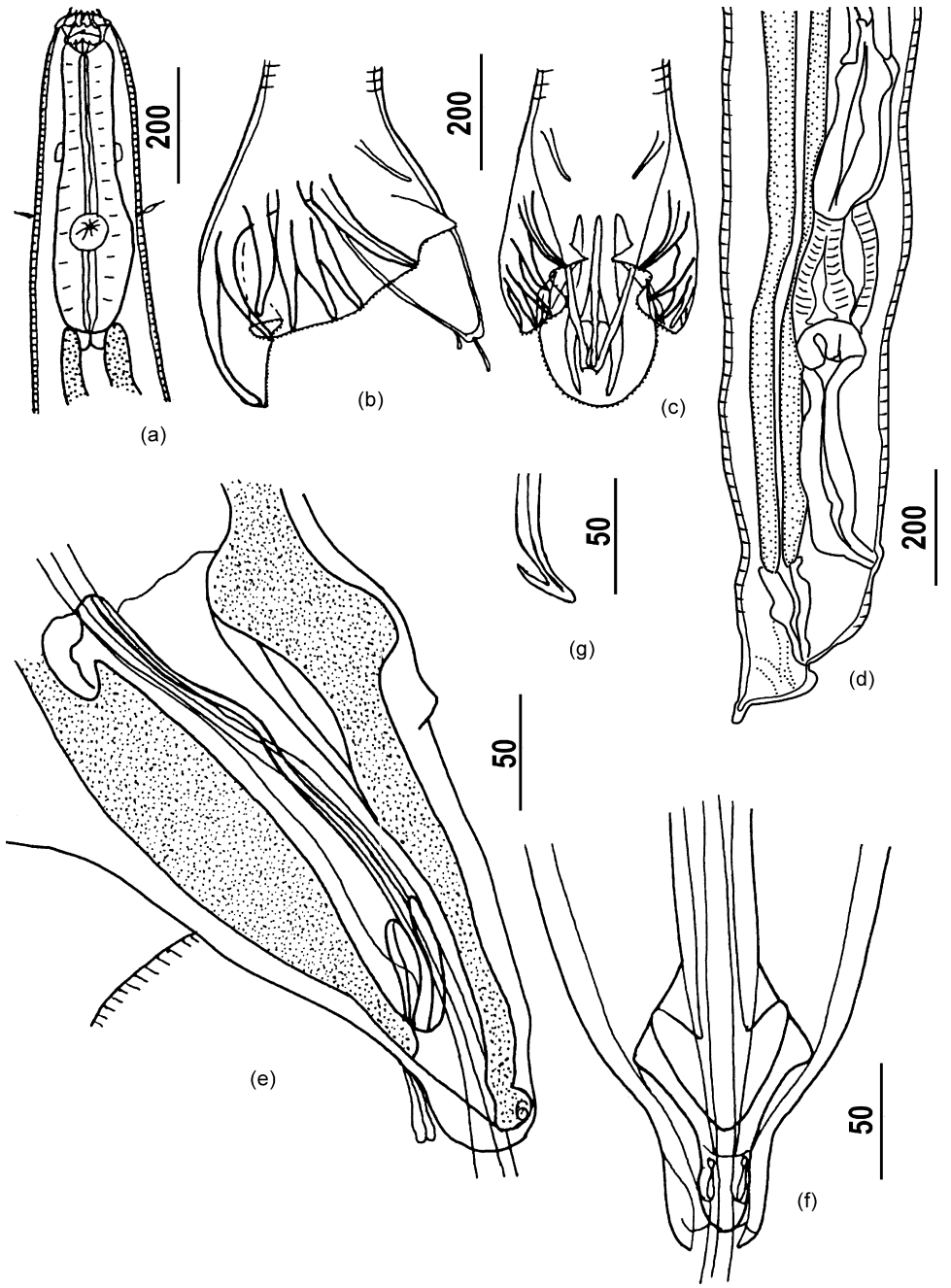

Fig. 65. *Skrjabinodentus tshoijoi.* (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

rounded; insertion point at 1/4 or less of BC depth. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, elongate, curving, thin at one end or short, triangular in optical section. Septum intracoronare origin on support. Medial insertion of septum intracoronare situated anterior to junction of ELC and ILC. Walls of BC straight, of uniform thickness. Buccal cavity wider than deep, but wider anteriorly or posteriorly. Dorsal gutter slightly more than 1/2 of BC depth. Buccal teeth absent. Esophageal funnel greatly enlarged. Esophageal teeth not prominent. Anterior muscular portion of esophagus about 1/4–1/3 of esophagus length.

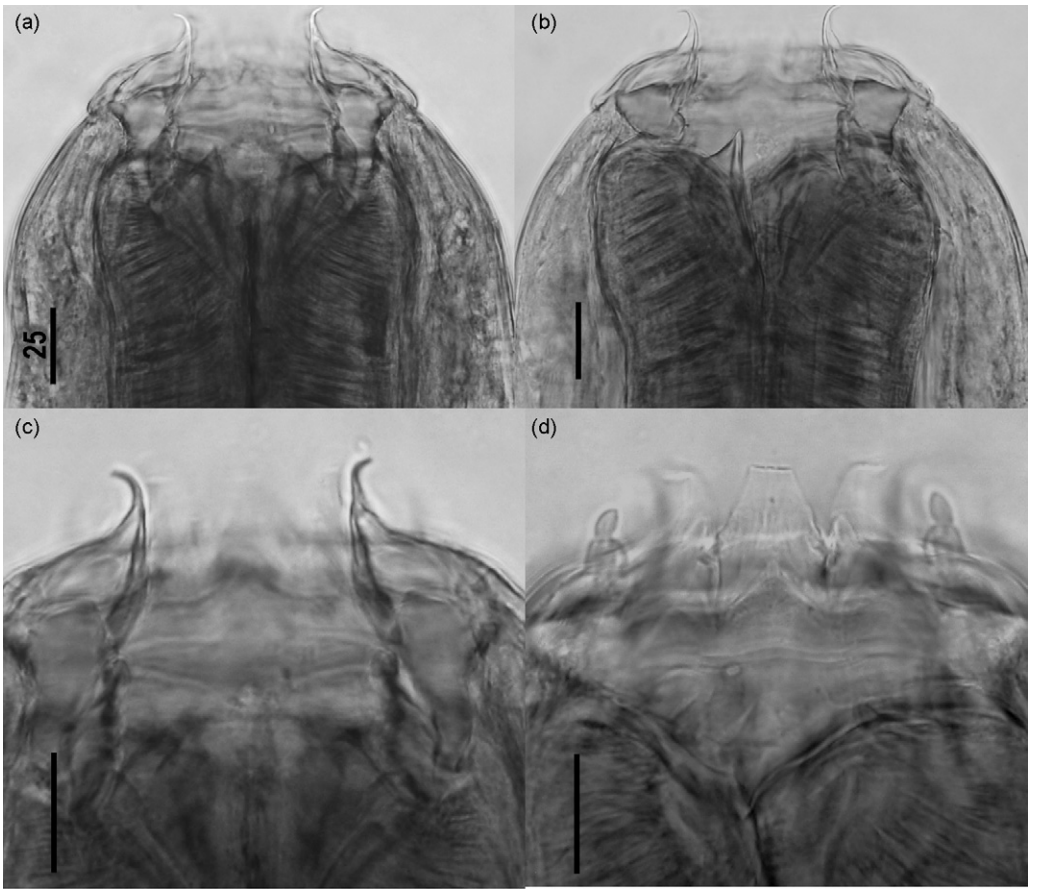

Fig. 66. *Skrjabinodentus tshoijoi.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing dorsal esophageal tooth on left. (c) Buccal cavity, dorsoventral view, showing short, broad dorsal gutter. (d) Buccal cavity, showing submedian papillae and elements of ELC and ILC.

Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches. Ventral rays shorter than laterals. Dorsal lobe longer then lateral lobes. Externodorsal rays origin at junction of dorsal and laterals rays. Gubernaculum large, with large dorsal handle and ventral notch. Genital cone short, conical or elongate, extends beyond bursal edge. Spicule tips pick-shaped.

Female. Vulva about one, or less than one, tail length from anus. Ovejector vestibule oval or Y-shaped, infundibulum about equal to sphincter. Tail conical or digitiform, short, length less than 2× diameter at anus.

Type species. *C. bicoronatus* (Looss, 1900) Cram, 1924

6.5.1. Key to species of Cylicodontophorus

(1) a. Buccal cavity wider anteriorly	*C. bicoronatus*
b. Buccal cavity wider posteriorly	*C. reineckei*

6.5.2. *C. bicoronatus (Looss, 1900) Cram, 1924 (Figs. 67 and 68)*

Synonyms. *Cyathostomum bicoronatum* Looss, 1900; *Cylichnostomum bicoronatum* (Looss, 1900) Looss, 1902; *Cylicostomum bicoronatum* (Looss, 1900) Gedoelst, 1903; *Trichonema bicoronatum* (Looss, 1900) Le Roux, 1924.

General. Medium-sized Cyathostominea. Posterior edge of MC situated anterior to edge of BC. Tip of submedian papillae bullet-shaped, two times as long as thick. ELC and ILC nearly equal in number of elements (26–30) and in length, but ILC slightly longer. Tips of elements of ILC pointed. Support for ELC continuous with BC, elongate, curving, thin at one end. Buccal cavity wider anteriorly. Deirids and excretory pore near middle of glandular esophagus, 430–487 from anterior end.

Male. Body length 9.1–11.8 mm. Esophagus length 550–730. BC width 69–100, depth 24–29. Spicule length from 1.75 to 2.1 mm. Gubernaculum length 280–307. Dorsal ray length (from distal tip to origin of

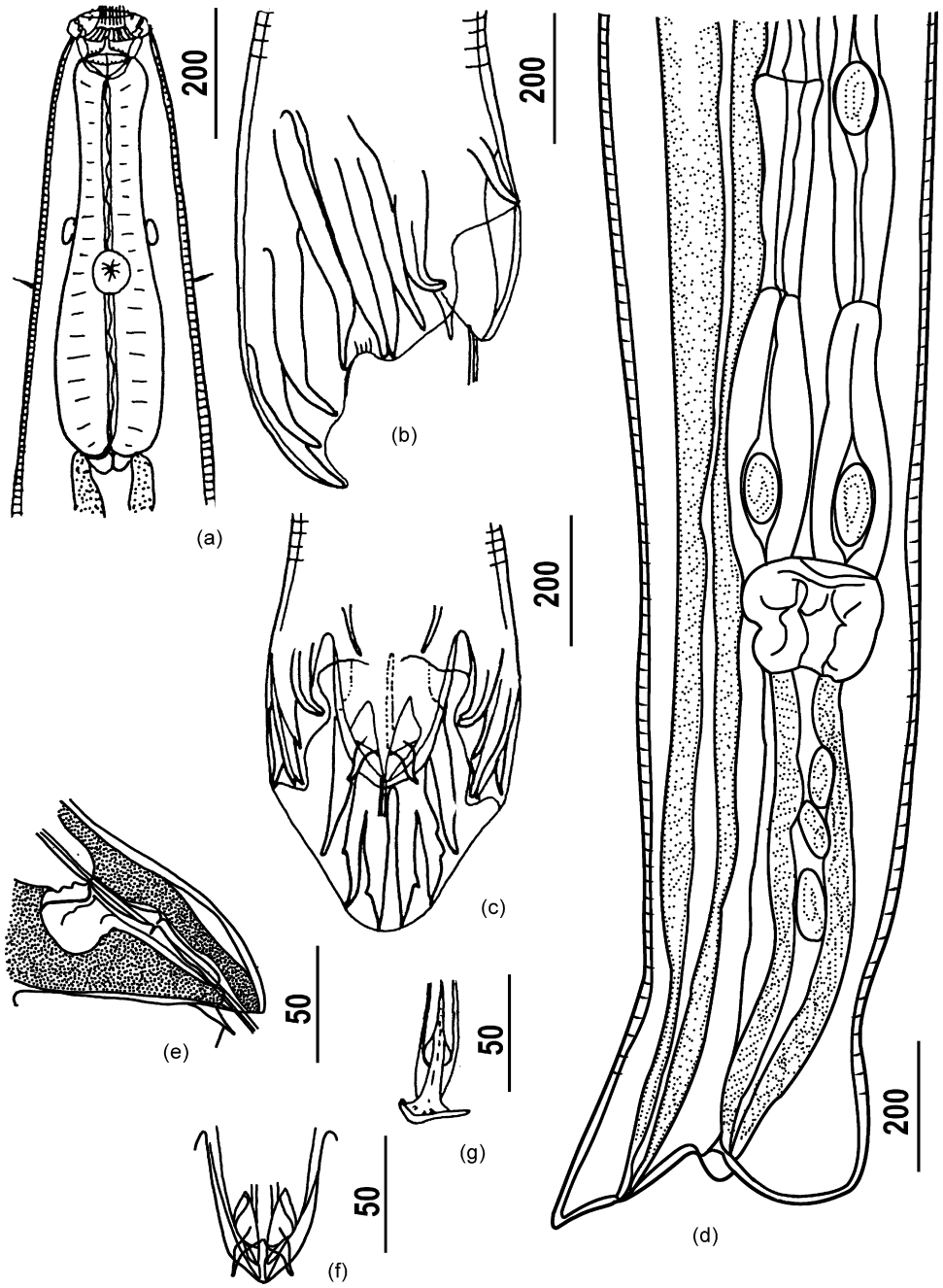

Fig. 67. *Cylicodontophorus bicoronatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

externodorsal ray) 480–615. Ventral rays length equal to laterals. Dermal collar poorly developed on ventral side of genital cone. Appendages of genital cone paired, large, finger-shaped, expanded proximally. Protrusions of dermal collar absent.

Female. Body length 11.8–14.5 mm. Esophagus length 680–770. BC width 74–102, depth 20–30. Vagina length 750–800. Vulva to tail tip 210–325. Anus to tail tip 60–140. Egg size 112–120 × 56–58.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

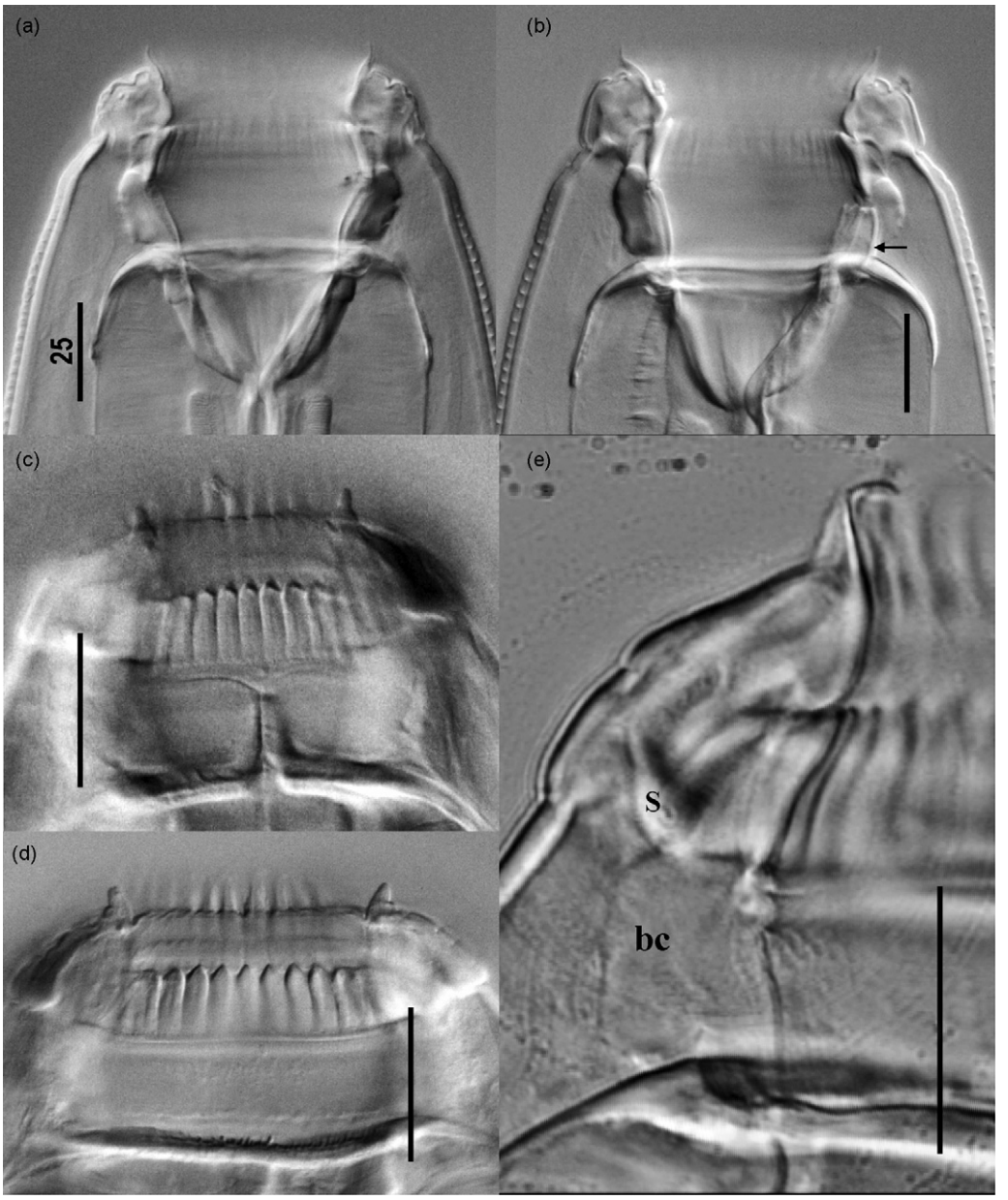

Fig. 68. *Cylicodontophorus bicoronatus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. Arrow marks dorsal gutter. (c) Dorsal gutter, elements of ILC and submedian papillae. (d) Elements of ILC and ELC and submedian papillae. (e) Buccal capsule, lateral view, showing wall of BC (bc), support (S) of ELC and elements of ILC and ELC.

6.5.3. C. reineckei Scialdo-Krecek and Malan, 1984 (Figs. 69 and 70)

General. Small-sized Cyathostominea. Posterior edge of MC situated posterior to edge of BC. Tip of submedian papillae bullet-shaped, round or oval, short. ELC elements more numerous (17–22) than ILC (15–19); and longer than ILC. Tips of elements of ILC rounded. Support for ELC short, triangular in optical section. Buccal cavity wider posteriorly. Deirids and excretory pore near middle of glandular esophagus, 240–449 from anterior end.

Male. Body length 7.2–12.3 mm. Esophagus length 558–752. BC width 39–53, depth 13–20. Spicule length 1.28–1.66 mm; distal tips spur-like. Gubernaculum length 237–252. Dorsal ray length 385–465. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone paired, finger-shaped. Protrusions of dermal collar absent.

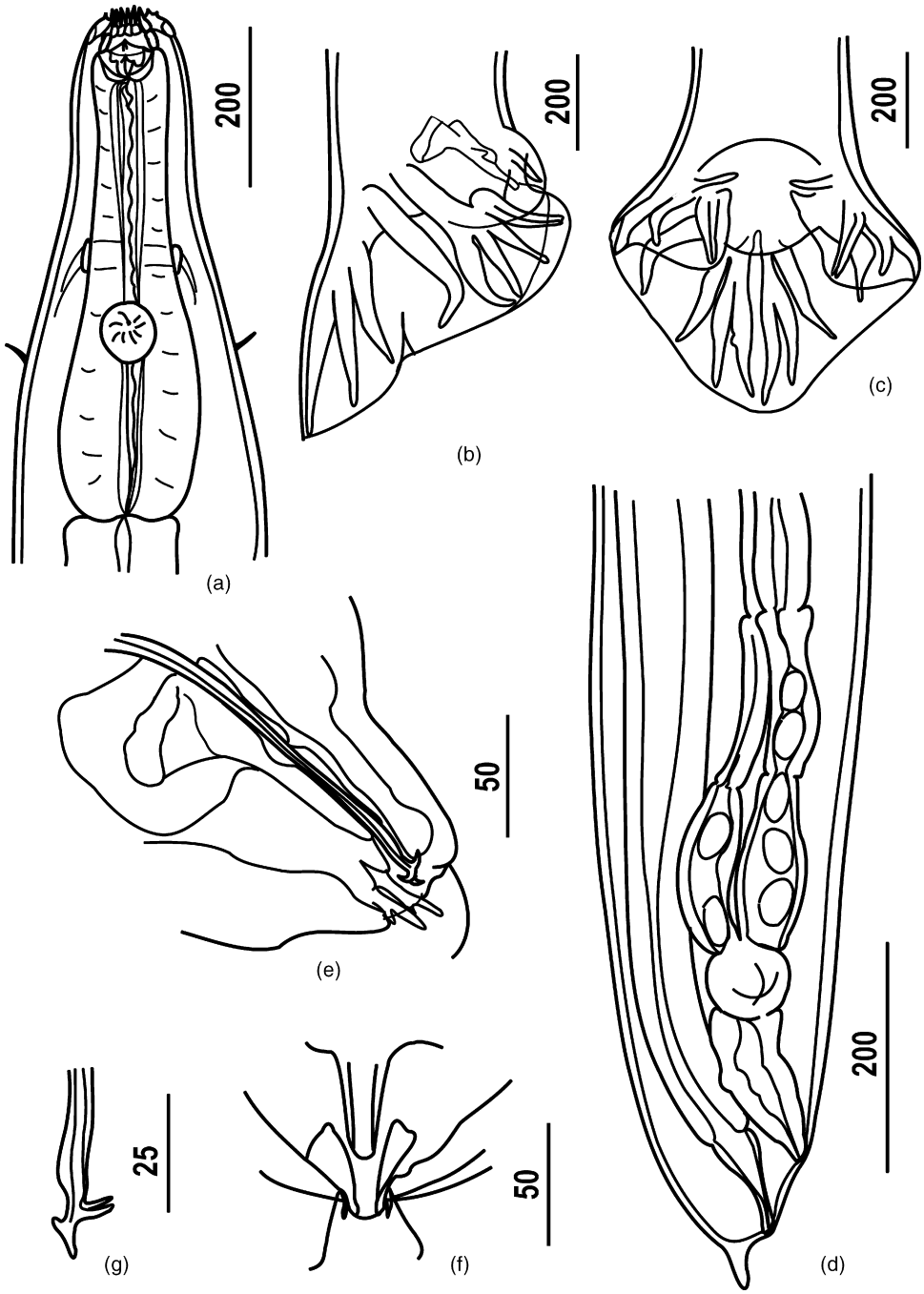

Fig. 69. *Cylicodontophorus reineckei*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male.

Female. Body length 10.9–15.7 mm. Esophagus length 640–778. BC width 46–52, depth 13–19. Vulva to tail tip 186–292. Anus to tail tip 79–133. Egg size 76–106 × 39–59.

Hosts. *E. burchelli*, *E. zebra hartmannae*.

Locality. Cecum, colon.

Distribution. Africa.

6.5.4. Discussion

This genus was proposed by Ihle (1922) and recognized by Theiler (1924) as a subgenus. Both workers included *C. bicoronatus, C. euproctus, C. ihlei*,

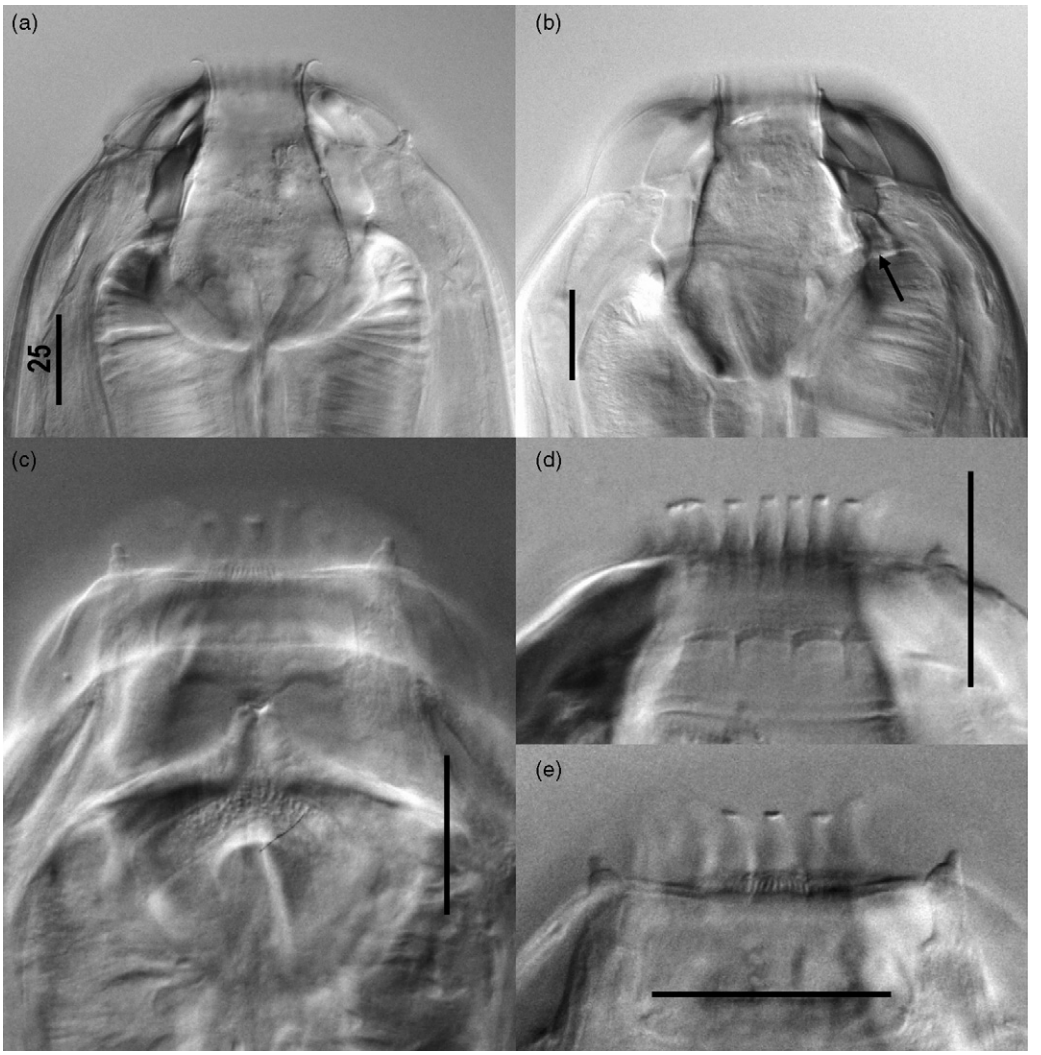

Fig. 70. *Cylicodontophorus reineckei*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. Arrow marks dorsal gutter. (c) Buccal capsule, dorsoventral view showing submedian papillae and dorsal gutter. (d) Elements of ILC and ELC. (e) Submedian papillae and elements of ELC.

and *Cylicocyclus ultrajectinus*. Cram (1924) raised Ihle's subgenus to the rank of genus and included the same four species. Ershov (1943) and Popova (1958) expanded the genus *Cylicodontophorus*, including three of the above-mentioned four species (excluding *C. ultrajectinus*) and adding *Cyathostomum sagittatum*, *Cyathostomum ornatum*, *Cyathostomum pateratum*, and *C. mettami*. These workers considered *C. ihlei* to be a junior synonym of *C. mettami*. K'ung (1964) considered the genus to have been improperly expanded and included only *C. bicoronatus, C. euproctus*, and *C. mettami*. Lichtenfels (1975) agreed with K'ung in this opinion. Dvojnos and Kharchenko (1988) redescribed *C. mongolica* Tschoijo, 1957. Another species previously included in this genus, *C. schuermanni* (Ortlepp, 1962), is known only from zebras.

Hartwich (1986) removed all except the type species to a new genus, *Parapoteriostomum*. We agree with Hartwich's (1986) restriction of *Cylicodontophorus* to species with the number of ILC and ELC elements about equal and with the ELC of broad pointed elements. We add to the single species retained by Hartwich, *C. bicoronatus*, a species not considered by Hartwich, *C. reineckei* Krecek et al., 1984. Zhang and K'ung (2002) placed *C. reineckei* in the genus *Parapoteriostomum.*

6.5.5. *Tridentoinfundibulum Tshoijo in Popova (1958)*

General. Middle-sized Cyathostominae. MC flattened, divided into inner and outer rings. Posterior edge of MC posterior to anterior edge of BC. Amphids not

markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae bulbous, twice as long as thick. Stalk of submedian papillae broader than long. Elements of ELC longer than broad, tips pointed; insertion point on tips of ILC. Elements of ILC difficult to distinguish, slightly longer than broad, identical in number to ELC; insertion point at 1/4 or less of BC depth. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, elongate, curving, thin at one end. Septum intracoronare origin on support. Medial insertion of septum intracoronare anterior to junction of ELC and ILC. Walls of BC straight, thicker in middle. Buccal cavity wider than deep, cylindrical. Dorsal gutter short, broad at base, less than 1/2 of BC depth. Buccal teeth absent. Esophageal funnel enlarged, especially in dorsal sector which forms invagination containing three esophageal teeth. Anterior muscular portion of esophagus about 1/4−1/3 of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches. Ventral rays shorter than laterals. Dorsal lobe longer then lateral lobes. Externodorsal rays origin at junction of dorsal and laterals rays. Gubernaculum large, with dorsal handle and ventral notch. Genital cone short, conical. Spicule tips hook- or harpoon-shaped

Female. Vulva more than one tail length from anus. Vagina shorter than sphincter of ovejector. Ovejector vestibule oval or Y-shaped, infundibulum longer than sphincter. Tail conical, short, length less than 2× diameter at anus.

Type species. *T. gobi* Tshoijo in Popova (1958).

6.5.6. *T. gobi Tshoijo in Popova, 1958 (Figs. 71 and 72)*

Synonyms. *Cylicostephanus torbertae* Lichtenfels and Klei, 1988.

General. With characteristics of the genus. ELC elements number 30–40, longer than broad, longer than ILC, tips pointed, insertion point on tips of ILC. Elements of ILC identical in number to ELC or may appear to merge into ring.

Male. Body length 10–12 mm. Esophagus length 643–646. BC width 116–118, depth 25–30. Deirids and excretory pore to head end 399–522. Spicule length 1.14–1.30 mm. Gubernaculum length 241–244. Dorsal ray length (tip to base of externo-dorsal ray) 715–742. Dermal collar well-developed around genital cone. Appendages of genital cone paired finger-shaped. Nipple like protrusions of dermal collar lateral to appendages.

Female. Body length 13–16 mm. Esophagus length 664–726. BC width 113–125, depth 29–33. Deirids and excretory pore to head end 312–555. Vulva to tail tip 1.04–1.08 mm. Anus to tail tip 332–457. Egg size 114–133 × 57–65. Tail conical, short.

Hosts. *Equus caballus*, *E. caballus* × *E. asinus*.

Locality. Cecum, colon.

Distribution. Asia, Europe, North America.

6.5.7. *Discussion*

Much remains to be learned about the generic relationships of this species, only recently described in enough detail to be recognized (Dvojnos and Kharchenko, 1994). This is a species that has been collected in Asia, North America and Europe (Lichtenfels et al., 1998). Lichtenfels and Klei (1988) described this species as *Cylicostephanus torbertae*. *Tridentoinfundibulum* is recognized at genus level herein because it appears on the basis of molecular phylogenies (McDonnell et al., 2000; Hung et al., 2000), to be within a clade that includes *Cylicostephanus* and *Cylicodontophorus*, but basal and separate from the species of those genera. Hartwich (1986) did not study this species.

6.6. *Petrovinema Ershov, 1943*

General. Middle- to large-sized Cyathostominea. MC flattened, divided into inner and outer rings. Posterior edge of MC at anterior edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae spindle-shaped or bullet-shaped, two to three times as long as thick. Stalk of submedian papillae longer than broad. Elements of ILC about three times as numerous as ELC; nearly equal in length. Elements of ELC longer than broad, tips pointed; insertion point on tips of ILC. Elements of ILC rod-shaped, longer than broad, tips rounded; insertion point on anterior edge of BC. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, elongate, curving, thin at one end. Septum intracoronare origin on support. Medial insertion of septum intracoronare situated at junction of ELC and ILC. Walls of BC straight, thicker posteriorly. Buccal cavity deeper than wide or as deep as wide, cylindrical. Dorsal gutter nipple- or button-like. Buccal teeth absent. Esophageal funnel shallow. Esophageal teeth not prominent. Anterior muscular portion of esophagus about 1/4−1/3 of esophagus

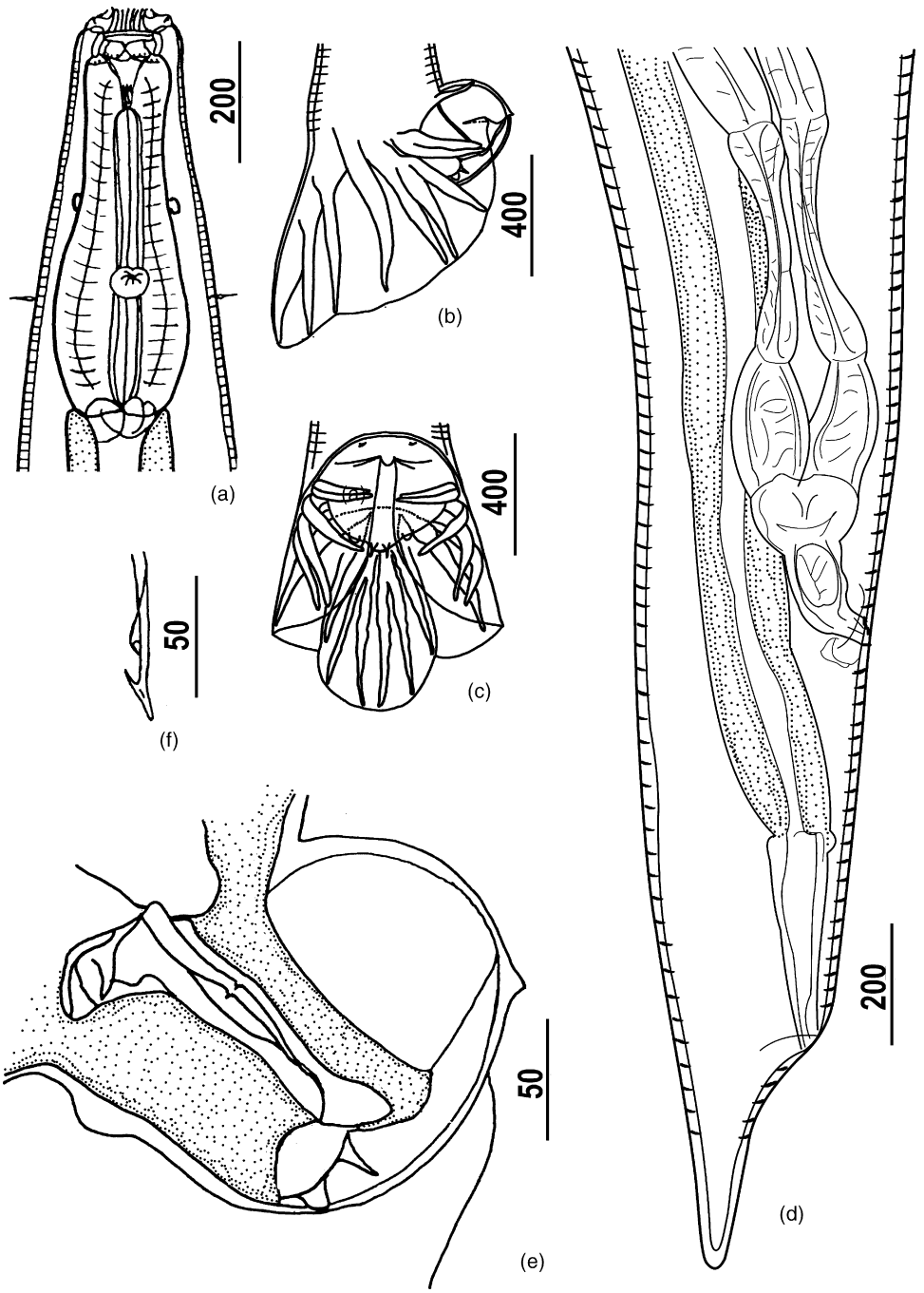

Fig. 71. *Tridentoinfundibulum gobi*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (e) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches. Ventral rays shorter than laterals. Dorsal lobe longer then lateral lobes. Externodorsal rays origin on stem of dorsal. Gubernaculum with small handle, enlarged distal tip. Genital cone elongate, extends beyond bursal edge. Spicule tips hook- or harpoon-shaped.

Female. Vulva about one, or less than one, tail length from anus. Vagina longer than sphincter of ovejector.

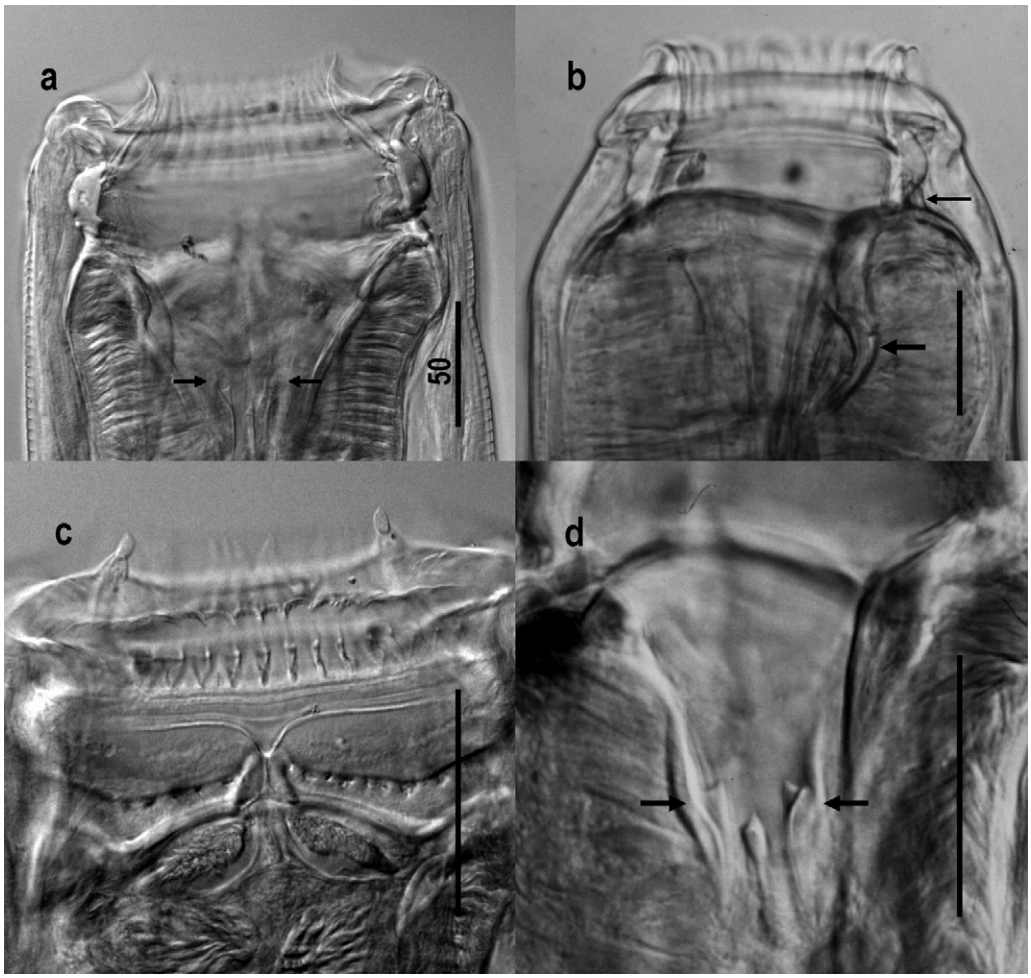

Fig. 72. *Tridentoinfundibulum gobi*. (a) Buccal capsule, dorsoventral view, showing three small esophageal teeth deep in dorsal sector of esophageal funnel (arrows). (b) Buccal capsule, lateral view, showing dorsal gutter (upper arrow) and dorsal invagination of esophageal funnel containing three esophageal teeth (lower arrow). (c) Elements of ELC and ILC, submedian papillae and dorsal gutter. (d) Esophageal funnel, dorsal view, showing three esophageal teeth deep in dorsal invagination (arrows).

Ovejector vestibule oval or Y-shaped, infundibulum longer than sphincter. Tail conical or digitiform, short or long.

Type species. *P. skrjabini* (Ershov, 1930) Ershov, 1943.

6.6.1. Key to species of Petrovinema

(1) a. Cuticular lining of BC without shelf-like projection. Esophageal funnel shallow. Dorsal lobe of male bursa long. Female tail digitiform, short	*P. skrjabini*
b. Cuticular lining of BC with shelf-like projection at half of BC depth. Esophageal funnel well-developed. Dorsal lobe of male bursa medium sized. Female tail conical, long	*P. poculatum*

6.6.2. *P. skrjabini (Ershov, 1930) Ershov, 1943 (Figs. 73 and 74)*

Synonyms. *Trichonema skrjabini* Ershov, 1930; *Cylicostephanus skrjabini* (Ershov, 1930) Lichtenfels, 1975.

General. Tip of submedian papillae bullet-shaped, two to three times as long as thick. ELC consists of 28 elements; ILC of 80. Tips of elements of ILC pointed. Medial insertion of septum intracoronare situated anteriorly to junction of ELC and ILC. Buccal cavity cylindrical, as deep as wide.

Male. Body length 14.2–14.3 mm. Esophagus length 672–756. BC width 132–216, depth 141–150. Anterior end to: deirids; excretory pore 616; NR 482–515. Spicule length 1.21–1.43 mm. Gubernaculum length 267–270. Dorsal ray length 560–644. Dermal collar

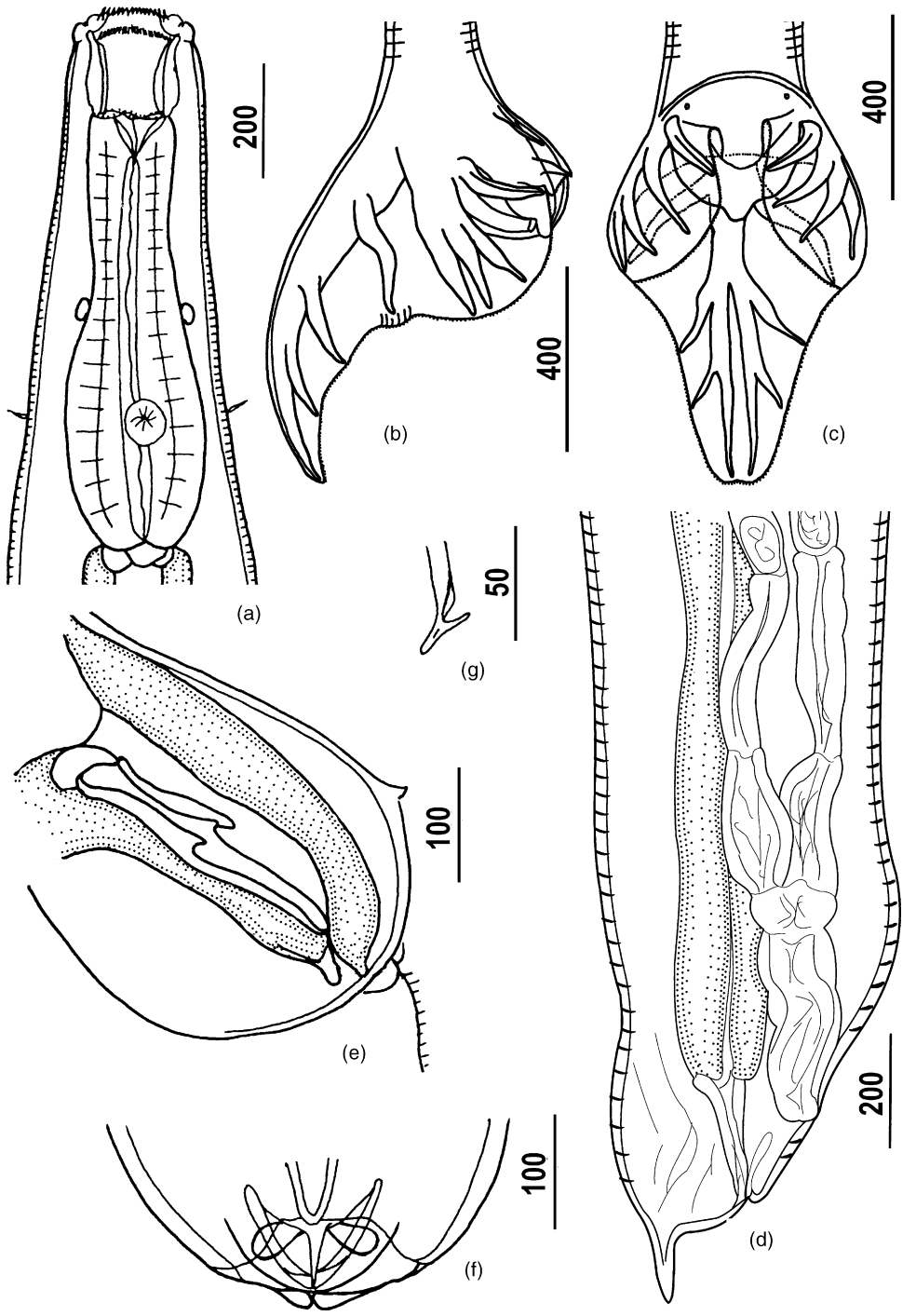

Fig. 73. *Petrovinema skrjabini.* (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

well-developed around genital cone. Appendages of genital cone paired, nipple-shaped. Protrusions of dermal collar wide and round, poorly developed.

Female. Body length 14.2–18.7 mm. Esophagus length 700–790. BC width 135–162, depth 144–165. Anterior end to: deirids 700–778; excretory pore 666–762; NR 498–538. Vagina length 291–392. Vulva to tail tip 347–459. Anus to tail tip 179–280. Egg size 117–130 × 52–56.

Hosts. *Equus caballus*, *E. asinus*.

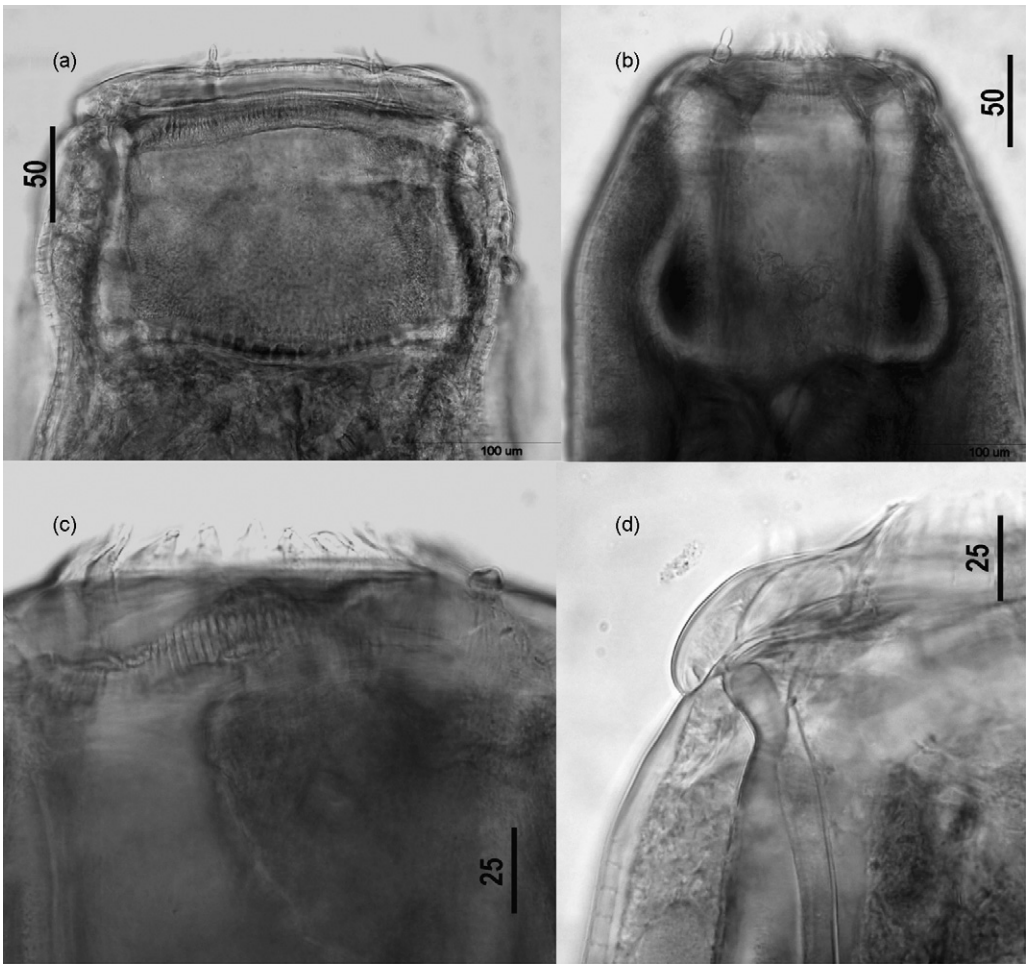

Fig. 74. *Petrovinema skrjabini*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Elements of ILC and ELC. (d) Buccal capsule, lateral view, showing support of ELC and bases of ELC and ILC.

Locality. Cecum, colon.

Distribution. Asia.

6.6.3. *P. poculatum (Looss, 1900) Ershov, 1943 (Figs. 75 and 76)*

Synonyms. *Cylicostephanus poculatus* (Looss, 1900) Cram, 1924; *Cyathostomum poculatum* Looss, 1900; *Cylichnostomum poculatum* (Looss, 1900) Looss, 1902; *Cylicostomum poculatum* (Looss, 1900) Gedoelst, 1903; *Trichonema poculatum* (Looss, 1900) Le Roux, 1924; *Petrovinema poculatum* (Looss, 1900) Ershov, 1943.

General. Tip of submedian papillae spindle-shaped, two to three times as long as thick. ELC consists 30–36 elements, ILC 84. Tips of ELC rounded. Medial insertion of septum intracoronare situated at junction of ELC and ILC.

Male. Body length 8.0–9.8 mm. Esophagus length 771–853. BC width 84–96, depth 80–96. Anterior end to: deirids 470–556; excretory pore 464–551; NR 455–522. Spicule length 675–754. Gubernaculum length 131–151. Dorsal ray length (tip to base of externo-dorsal ray) 435–493. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone paired, delicate finger-shaped. Protrusions of dermal collar absent.

Female. Body length 10.5–12.5 mm. Esophagus 771–935. BC width 87–101, depth 92–102. Anterior end to: deirids 536–722; excretory pore 493–644; NR 595. Vagina length 290–328. Vulva to tail tip 492–574. Anus to tail tip 328–377. Egg size 61–73 × 32–44.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

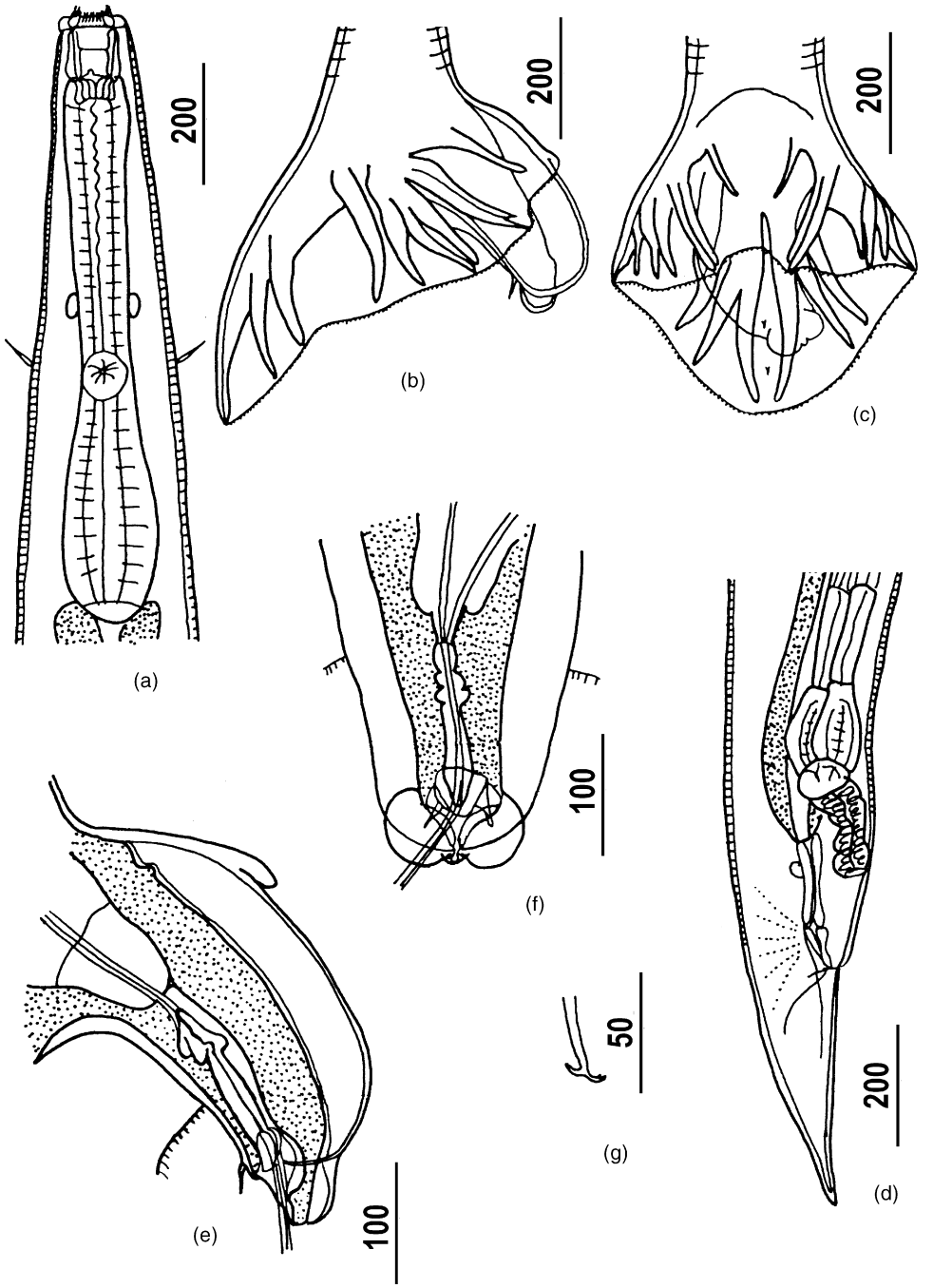

Fig. 75. *Petrovinema poculatum.* (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

6.6.4. Discussion

Previously Lichtenfels (1975) included the two species of *Petrovinema* in *Cylicostephanus*, but the characteristics of the mouth collar, buccal capsule wall and support of the ELC described by Hartwich (1986) do not support retaining *Petrovinema* in *Cylicostephanus*. The molecular data of Hung et al. (2000) supports the recognition of *Petrovinema* as a separate genus, basal to the rest of the Cyathostominea.

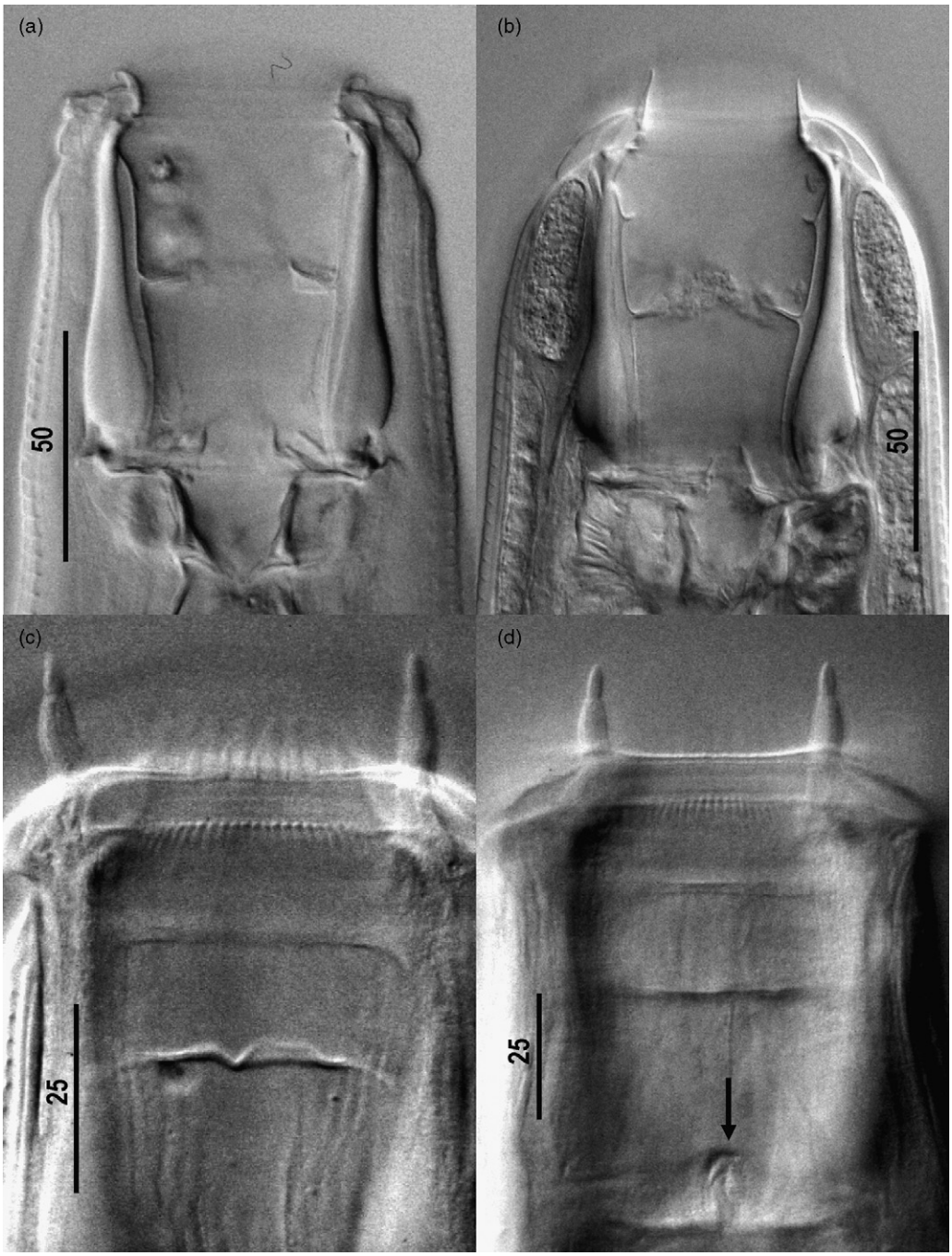

Fig. 76. *Petrovinema poculatum.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Submedian papillae, elements of ILC and ELC and cuticular shelf of lining of BC. (d) Submedian papillae, elements of ILC and dorsal gutter (arrow).

6.7. *Cylicocyclus* Ihle, 1922

Synonyms. *Cylicostomum* (*Cylicocyclus*) Ihle, 1922; *Cylicobrachytus* Cram, 1924; *Schulzitrichonema* Ershov, 1943.

General. Small or medium-sized Cyathostominae. MC inflated, high, ring-shaped, divided into inner and outer rings. Posterior edge of MC anterior to anterior edge of BC. Amphids project above MC surface. Tips and longer stalks of submedian papillae extend through MC.

Tips of submedian papillae spindle- or bullet-shaped, or uniform thickness two to three times or more as long as thick. Stalks of submedian papillae longer than broad or broader than long. ELC elements markedly less numerous and longer than ILC elements. Elements of ELC longer than broad, tips rounded or pointed; insertion point on tips of ILC. Elements of ILC longer than broad, tips rounded; insertion point on anterior edge of BC. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, elongate, curving, thin at one end. Septum intracoronare origin on support. Medial insertion of septum intracoronare anterior to junction of ELC and ILC. Walls of BC concave or straight, with prominent ring-like thickening at base. Buccal cavity cylindrical, wider than deep. Dorsal gutter button-like or 1/2 or less of BC depth. Buccal teeth absent. Esophageal funnel shallow or enlarged. Esophageal teeth prominent or not. Anterior muscular portion of esophagus about 1/4−1/3 of esophagus length. Excretory pore posterior to NR or near EI. Deirids at level of NR, near middle of glandular esophagus or posterior to EI.

Male. Dorsal ray with six branches. Ventral bursal rays shorter or equal to laterals. Dorsal bursal lobe longer then laterals. Gubernaculum large, with dorsal handle and ventral notch. Genital cone short, conical. Spicule tips pick-shaped.

Female. Vulva about one, or less than one, tail length from anus. Vagina longer than sphincter. Ovejector vestibule oval or Y-shaped; infundibulum equal to, or longer than, sphincter. Tail digitiform, short, length less than 2× diameter at anus.

Type species. *C. radiatus* (Looss, 1900) Chaves, 1930

6.7.1. Key to species of Cylicocyclus

(1)	a. Buccal capsule extremely shallow with very delicate inconspicuous walls	*C. brevicapsulatus*
	b. Buccal capsule not extremely shallow or delicate	2
(2)	a. Both lateral papillae and ELC prominent, extending beyond mouth collar	3
	b. Either lateral papillae or ELC may be prominent, but not both	6
(3)	a. Dorsal gutter extends for 1/2 of depth of buccal cavity. ELC consists of 20 elements. Cuticular lining of BC with internal, shelf-like projection	*C. nassatus*
	b. Dorsal gutter short, little more than a button. ELC consists of more than 20 elements. Cuticular lining of BC without internal, shelf-like projection	4
(4)	a. ELC consists about 40–46 elements. Female tail club-shaped. Male genital cone not covered by lateral lobes of bursa	*C. asini*
	b. ELC consists about 30 elements. Female tail straight. Male genital cone covered by lateral lobes of bursa	5
(5)	a. Dorsal and ventral notches on mouth collar absent. Appendages of genital cone oval with finger-shaped projections	*C. ashworthi*
	b. Dorsal and ventral notches on mouth collar present Appendages of genital cone semilunar plates	*C. triramosus*
(6)	a. Lateral papillae extremely long, earlike or hornlike, extend much higher than mouth collar and submedian papillae. Excretory pore and cervical papillae posterior to EI	*C. auriculatus*
	b. Lateral papillae not extremely long. Excretory pore and cervical papillae at or anterior to EI	7
(7)	a. Excretory pore and cervical papillae near EI	8
	b. Excretory pore and cervical papillae well anterior to EI	10
(8)	a. ELC elements broad, numbers 10–12. ILC elements as long or longer than ELC elements; 12 of 46 ILC elements longer than others	*C. ultrajectinus*
	b. ELC elements narrow, number about 38 in males and 44 in females. ILC elements much shorter than ELC elements and of uniform length	9
(9)	a. Parasite of horses. Spicule length 2.6–3.4 mm. Genital cone with broad, rounded dorsal papillae and lateral spine. Vagina length 0.74–2.14 mm	*C. insigne*
	b. Parasite of zebra. Spicule length 2.1–2.6 mm. Genital cone with longer than wide dorsal papillae, without lateral spine. Vagina length 0.43–1.07 mm	*C. gyalocephaloides*
(10)	a. Esophageal funnel nearly as large as buccal capsule, with thick cuticular lining	11
	b. Esophageal funnel small, with thin cuticular lining	12
(11)	a. Dorsal gutter not apparent. Ring in base of buccal capsule well-developed. Esophagus greatly elongated with posterior half enlarged but cylindrical	*C. elongatus*
	b. Dorsal gutter button-like. Ring in base of buccal capsule poorly developed. Esophagus short, pyriform	*C. adersi*
(12)	a. Esophageal–intestinal valve elongated. Buccal cavity small, about 30 μm. deep by 60 μm wide. Wall of BC thickens gradually toward base without marked offset of ring. Dorsal gutter button-like but distinct	*C. leptostomum*

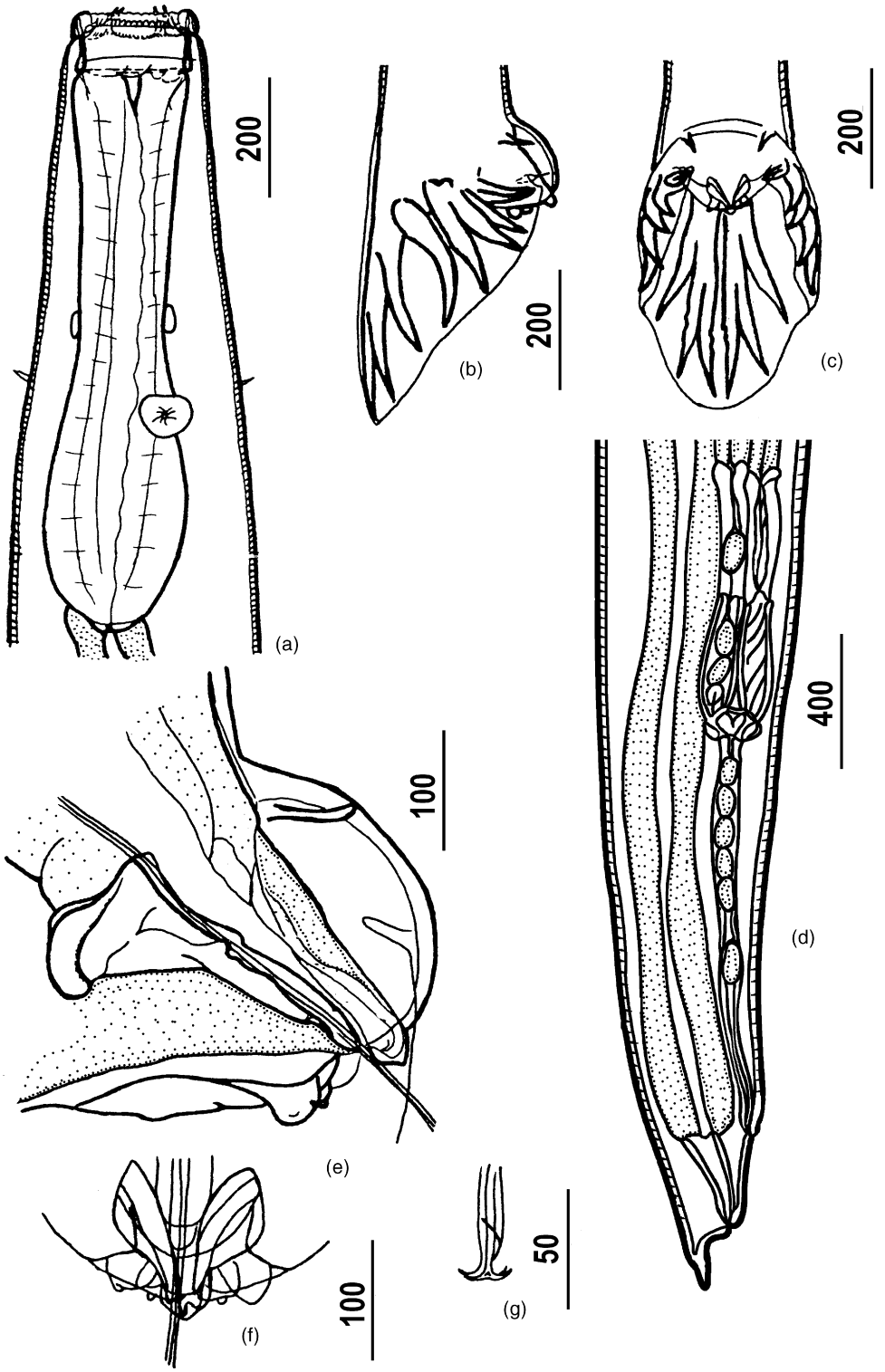

Fig. 77. *Cylicocyclus radiatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

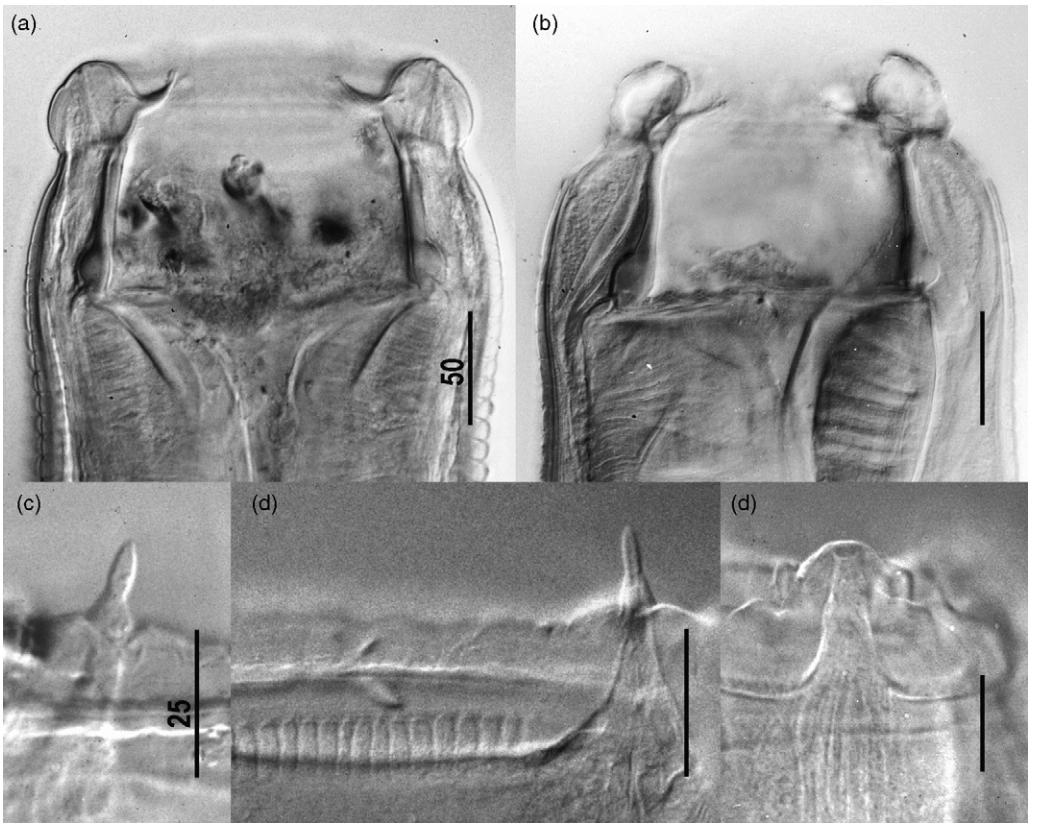

Fig. 78. *Cylicocyclus radiatus.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Submedian papilla. (d) Submedian papillae and elements of ILC. (e) Lateral papilla (a, b from Lichtenfels et al., 1998).

b. Esophageal–intestinal valve not elongated. Buccal cavity large, about 55 μm deep by 120 μm wide. Posterior ring of BC wall offset. Dorsal gutter not apparent	*C. radiatus*

6.7.2. *C. radiatus (Looss, 1900) Chaves, 1930(Figs. 77 and 78)*

Synonyms. *Cyathostomum radiatum* Looss, 1900; *Cylichnostomum radiatum* (Looss, 1900) Looss, 1902; *Cylicostomum radiatum* (Looss, 1900) Gedoelst, 1903; *Trichonema radiatum* (Looss, 1900) Le Roux, 1924; *Cylicostomum prionodes* Kotlán, 1921.

General. Posterior edge of MC situated at anterior edge of BC. Amphids project above MC surface. Tip of submedian papillae spindle-shaped, about four times as long as thick. Stalk of submedian papillae longer than broad. ELC markedly less numerous (26–28) and longer than ILC (50–60). Walls of BC concave. Posterior ring of BC wall offset. Buccal cavity cylindrical. Dorsal gutter not apparent. Esophageal funnel small, with thin cuticular lining. Excretory pore posterior to NR. Deirids near middle of glandular esophagus. Esophageal–intestinal valve not elongated.

Male. Body length 9.5–12.0 mm. Esophagus length 80–91. BC width 110–164, depth 50–60. Anterior end to deirids 454–675; to excretory pore 431–675; to nerve ring 401–506. Spicule length 1.75–1.89 mm; tips pick-shaped. Gubernaculum length 240–268. Dorsal ray length 574–789. Ventral rays shorter then laterals. Externodorsal rays origin at junction of dorsal and laterals rays. Genital cone appendages paired, bi-lobed, bubble-like, opaque, with tiny nipple-like points.

Female. Body length 13–14 mm. Esophagus length 800–910. BC width 140–176, depth 48–56. Anterior end to: deirids 438–686; excretory pore 412–690; NR 398–544. Vagina length 600–700. Vulva to tail tip 400–550. Anus to tail tip 200–270. Egg size 92–104 × 44–48. Tail digitiform.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

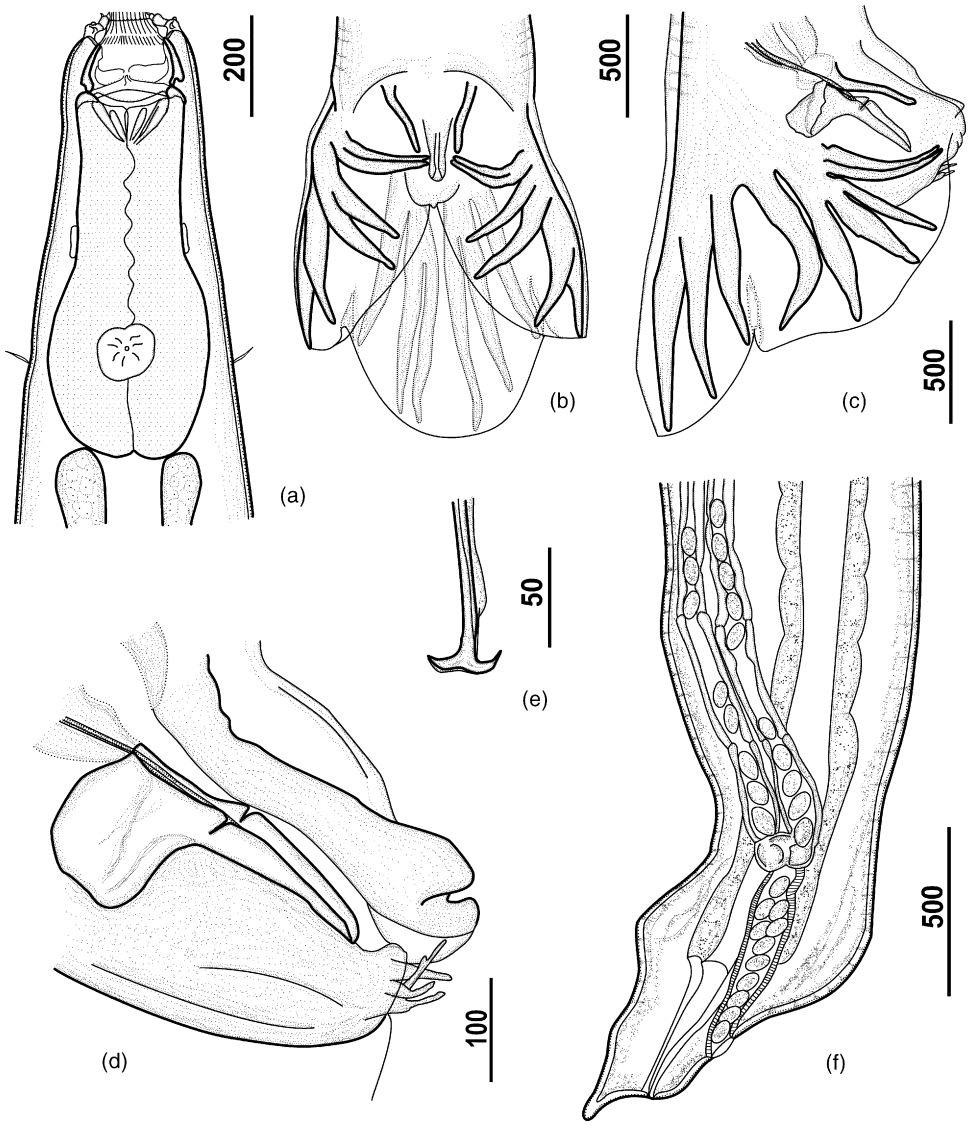

Fig. 79. *Cylicocyclus adersi.* (a) Esophageal region, ventral view. (b) Male tail, ventral view. (c) Male tail, lateral view. (d) Genital cone, lateral view. (e) Fused spicule tips of male. (f) Tail of female (from Kharchenko et al., 2004).

6.7.3. C. adersi (Boulenger, 1920) Chaves, 1930 (Figs. 79 and 80)

Synonyms. *Cylicostomum adersi* Boulenger, 1920; *Trichonema adersi* (Boulenger, 1920) Le Roux, 1924.

General. Amphids project slightly above MC surface. Tips of submedian papillae bullet-shaped, short. ELC elements markedly less numerous (30), and approximately twice as long, than elements of ILC (60). Elements of ELC longer than broad. Tips of elements of ILC pointed. BC walls concave. Buccal cavity wider posteriorly. Dorsal gutter button-like. Esophageal funnel greatly enlarged. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Body length 12.5–14.0 mm. Esophagus length 600–660. BC width 140–160, depth 60–72. Anterior end to: deirids 680; excretory pore 552–653; NR 331–429. Spicule length 1.2–1.4 mm; tips harpoon-shaped. Gubernaculum length 260–311. Dorsal ray length 675–750. Ventral rays length equal to laterals. Dermal collar poorly developed on ventral surface of genital cone. Appendages of genital cone oval plates with four finger-shaped projections, frequently bifurcated distally, fused medially. Protrusions of dermal collar present.

Female. Body length 14–16 mm. Esophagus length 640–720. BC width 140–160, depth 60–72. Anterior end to deirids and excretory pore 600–650. Vulva to

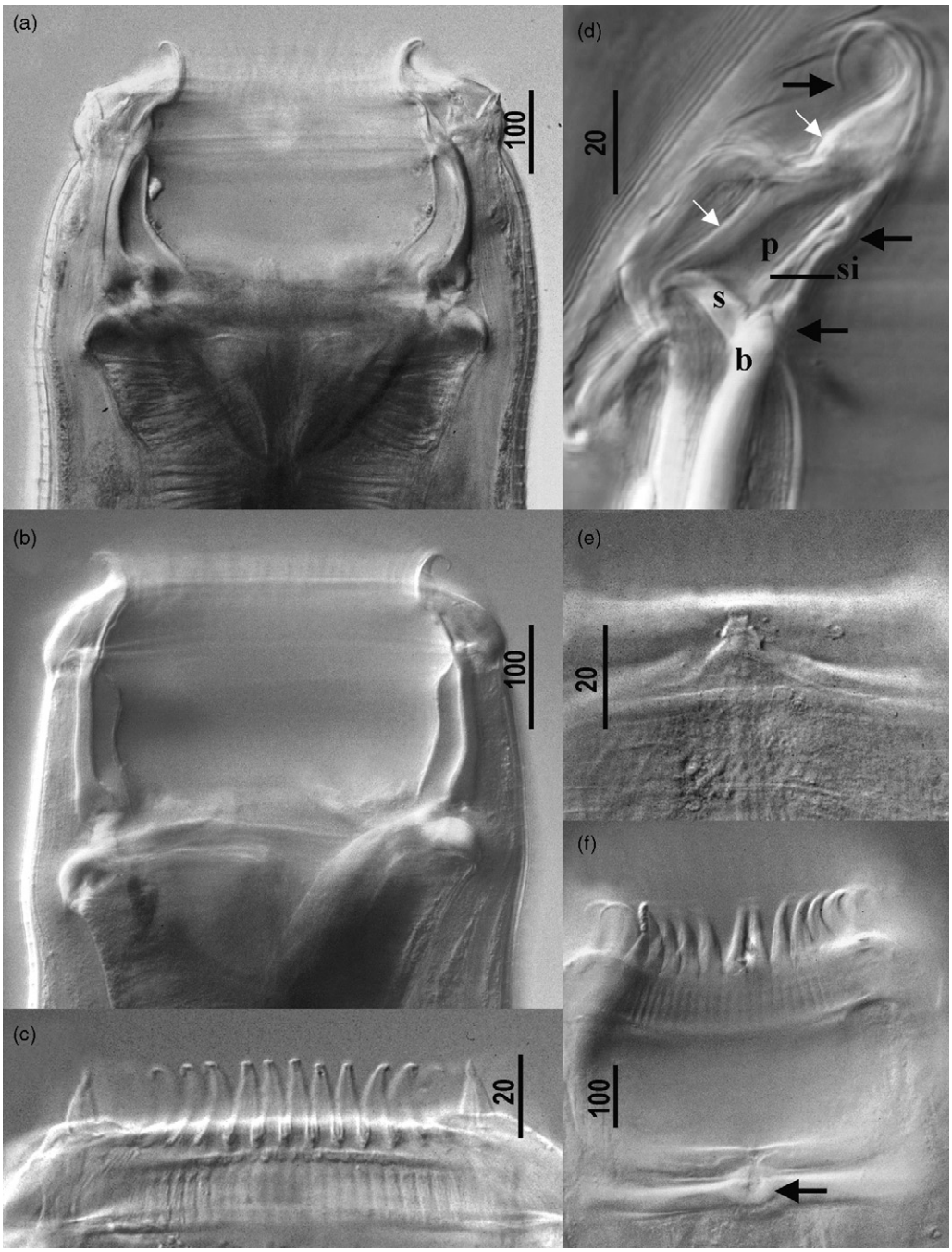

Fig. 80. *Cylicocyclus adersi.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Submedian papillae, elements of ILC and ELC, lateral view. (d) Mouth collar, lateral view, showing junction of inner and outer rings of mouth collar (white arrows), element of ELC (between top 2 black arrows), element of ILC (between lower 2 black arrows), support (s), anterior edge of buccal capsule (b), pulpa (p) and septum intracoronare (si). (e) Lateral papilla. (f) Dorsal gutter (arrow) and elements of ELC and ILC (from Kharchenko et al., 2004).

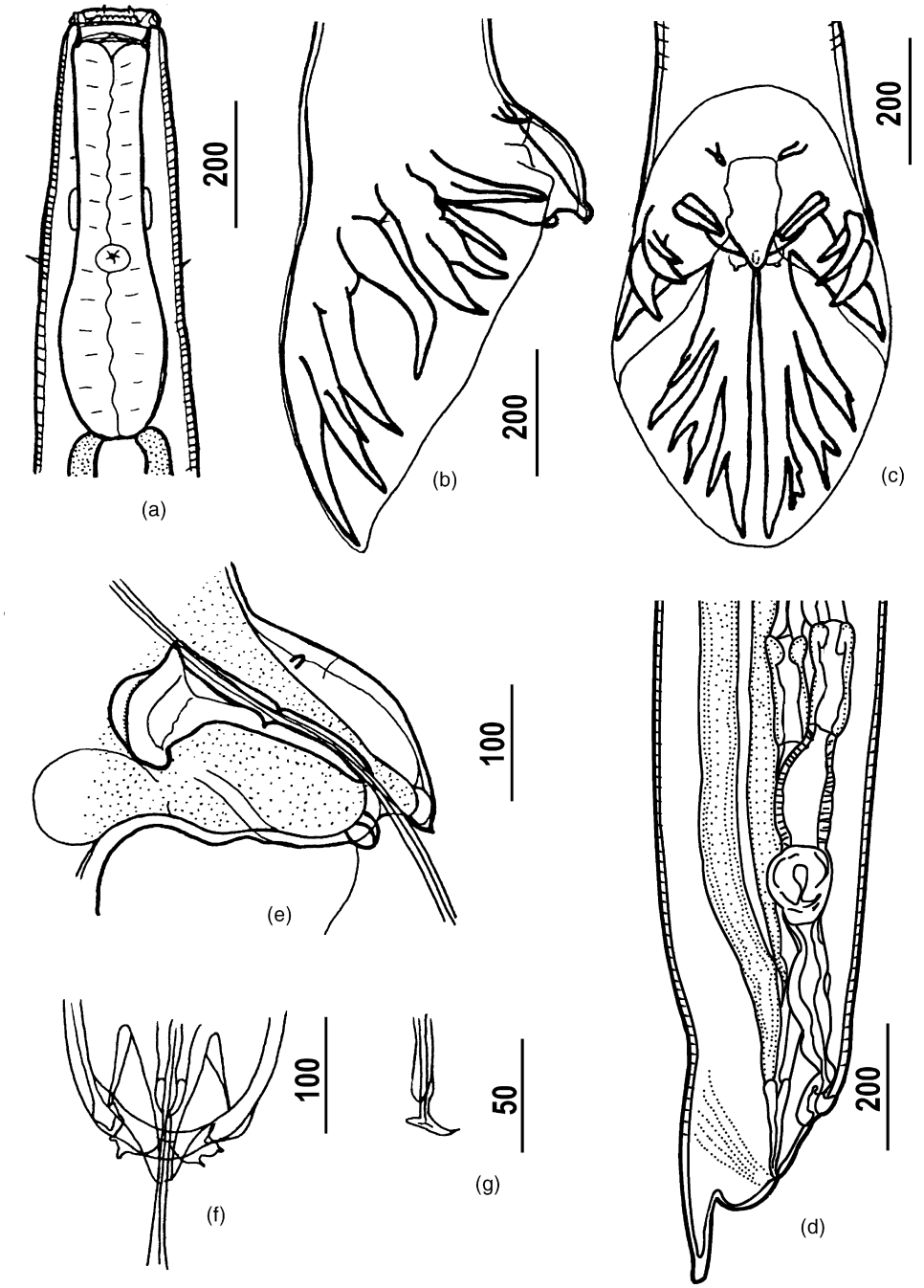

Fig. 81. *Cylicocyclus ashworthi.* (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male.

anus 366–427. Anus to tail tip 195–214. Vagina length 0.95–1.3 mm. Egg size 80–88 × 36–40.

Hosts. *E. asinus*, *E. burchelli* antiquorum, *E. zebra zebra*.

Locality. Cecum, colon.

Distribution. Africa.

6.7.4. C. ashworthi (Le Roux, 1924) McIntosh, 1933 (Figs. 81 and 82)

Synonyms. *Cylicostomum nassatum parvum* Yorke and Macfie, 1918; *Cylicocyclus largocapsulatus* (Iren, 1943) Lichtenfels, 1975; *Trichonema largocapsulatus* Iren, 1943; *Cylicocyclus matumurai* (Yamaguti, 1942)

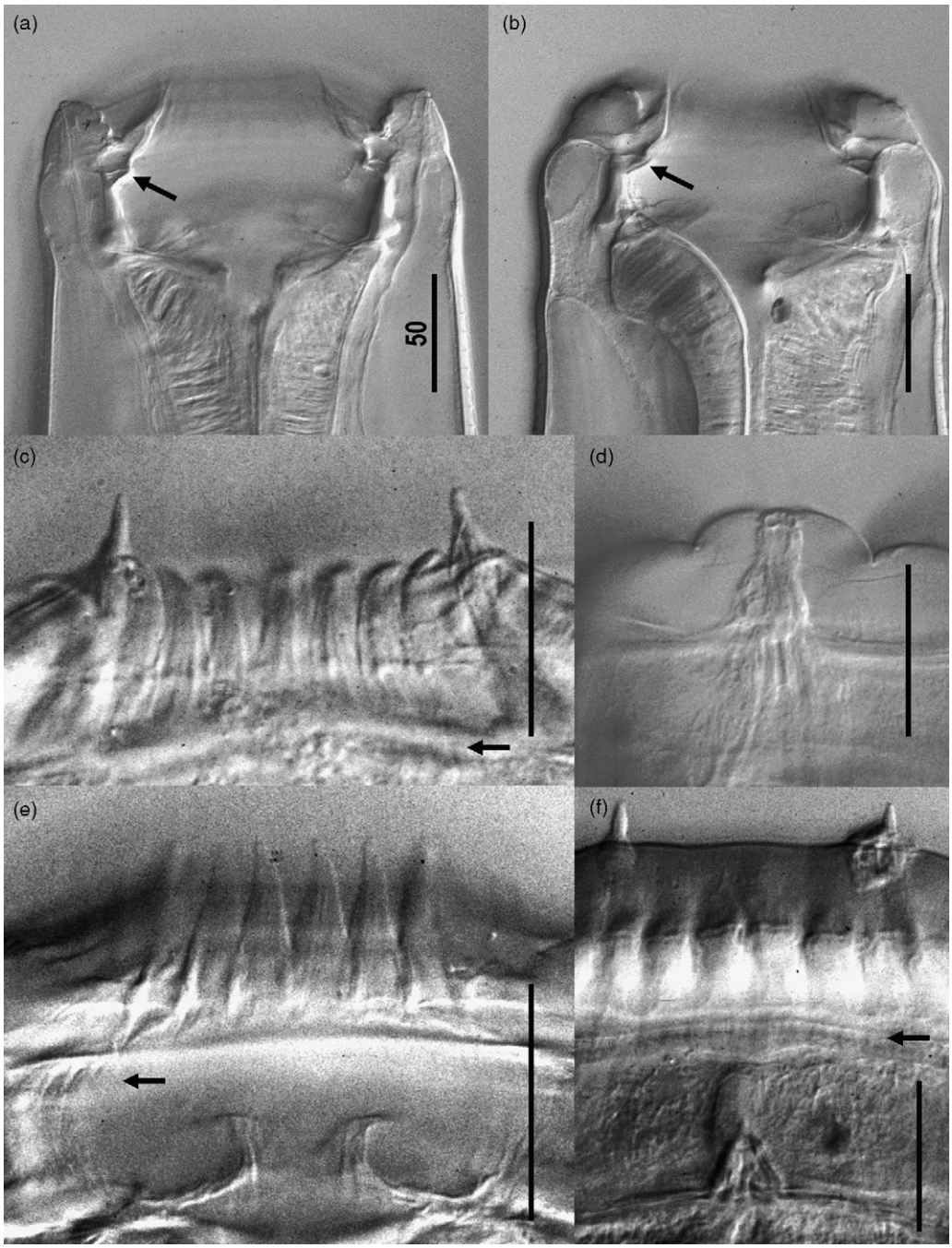

Fig. 82. *Cylicocyclus ashworthi.* (a) Buccal capsule, dorsoventral view. Arrow marks ILC. (b) Buccal capsule, lateral view. Arrow marks ILC. (c) Submedian papillae, elements of ILC (arrow) and ELC. (d) Lateral papilla. (e) Elements of ELC and ILC (arrow). (f) Submedian papillae, elements of ILC (arrow) and dorsal gutter.

Lichtenfels, 1975; *Trichonema matumurai* Yamaguti, 1942; *Cylicocyclus* (*Cylicobrachytus*) *zhidanensis*) Zang and Li, 1981.

General. Dorsal and ventral notches on mouth collar absent. Amphids project above MC surface. Tips of submedian papillae spindle-shaped, two to three times as long as thick. ELC of 25–29 elements; longer than numerous ILC elements. Tips of elements of ILC rounded. BC walls straight with posterior ring. Buccal cavity cylindrical. Dorsal gutter short,

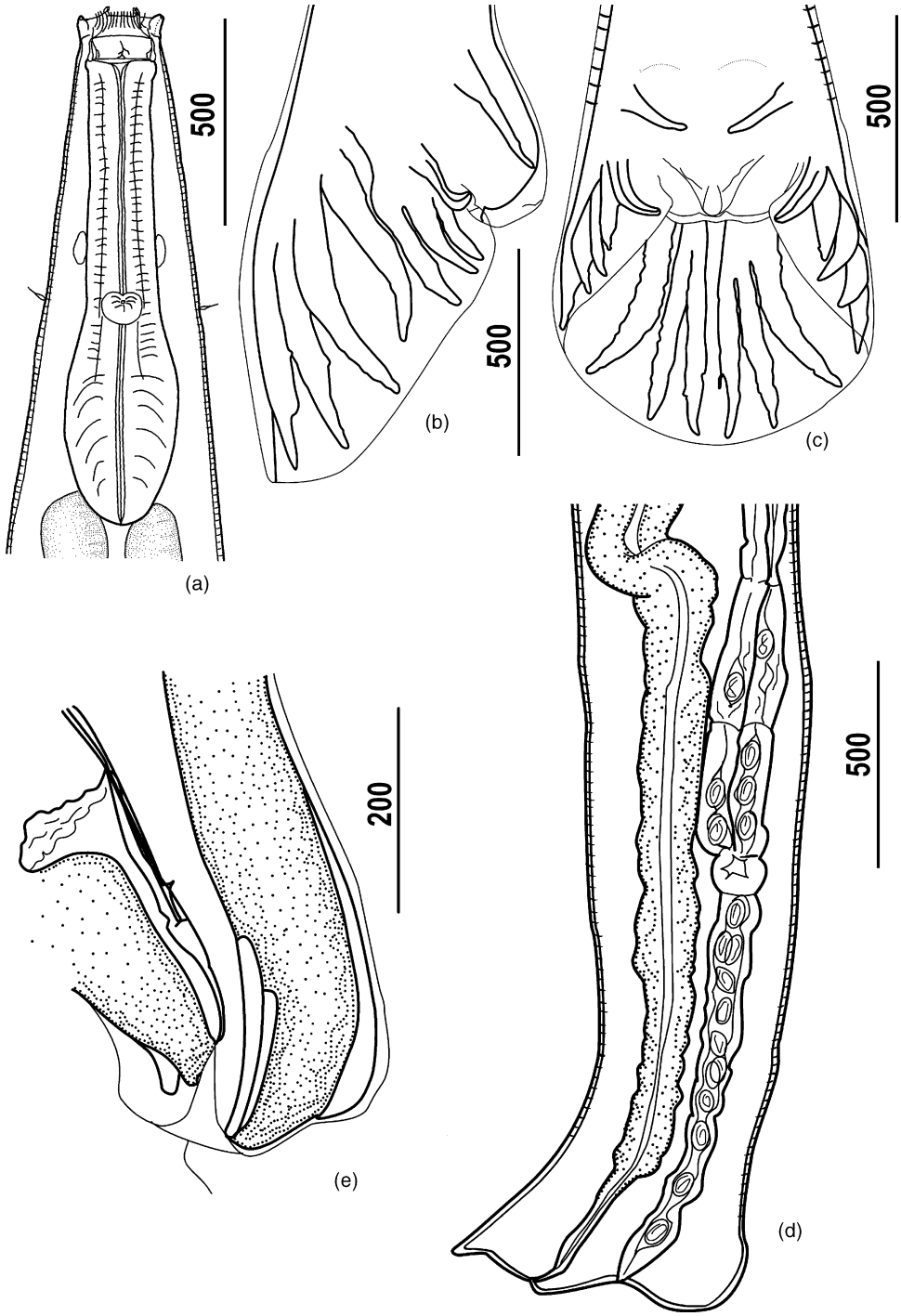

Fig. 83. *Cylicocyclus asini.* (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view.

triangular. Esophageal funnel shallow. Excretory pore posterior to NR. Deirids near middle of glandular esophagus. Esophageal–intestinal valve not elongated.

Male. Body length 8.2–9.5 mm. Esophagus length 648–680. BC width 90–124, depth 24–27. Anterior end to: deirids 426–498; excretory pore 403–504. Male genital cone covered by lateral lobes of

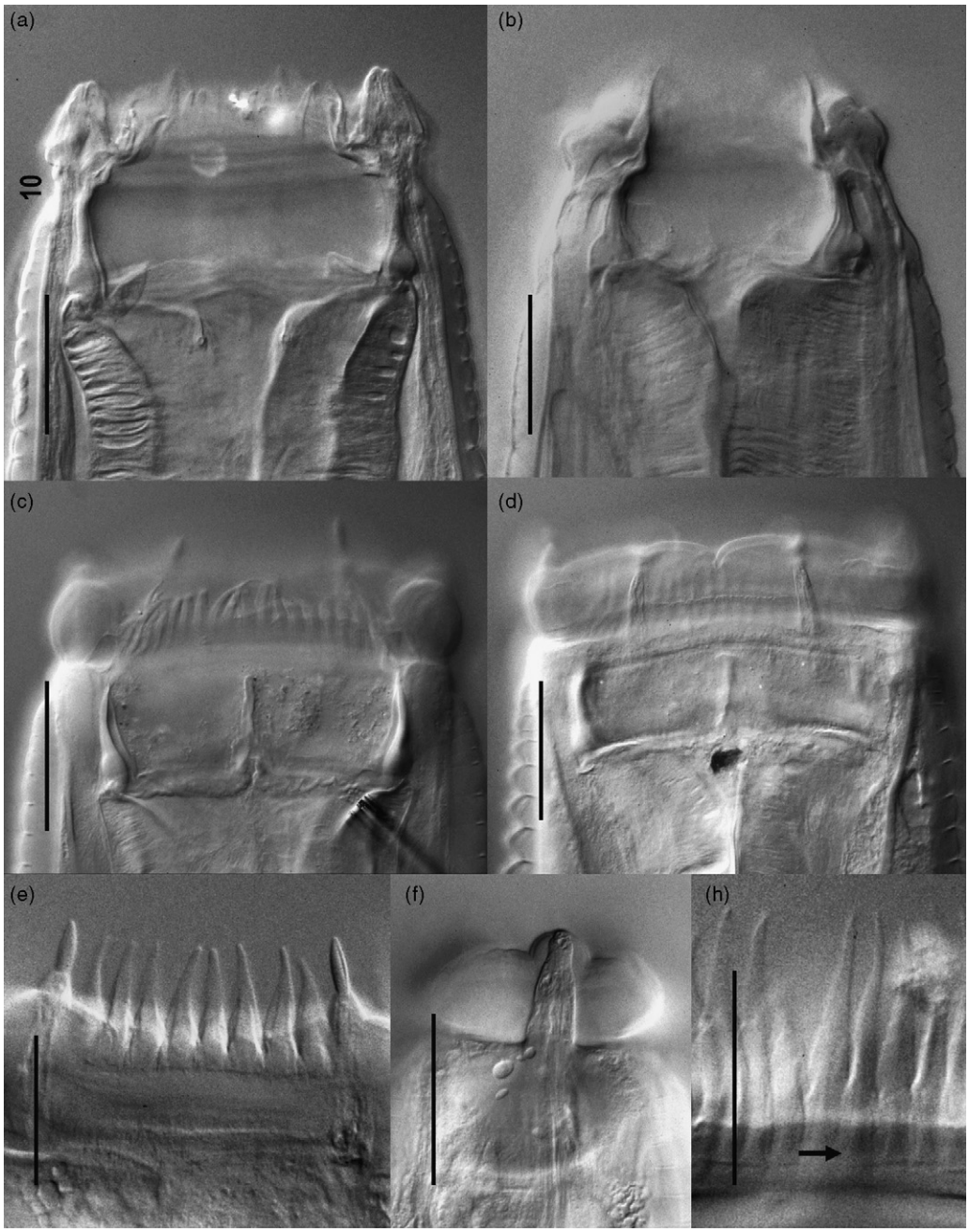

Fig. 84. *Cylicocyclus asini.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Dorsal gutter and ILC. (d) Dorsal notch in mouth collar. (e) Submedian papillae and elements of ELC. (f) Lateral papilla. (g) Elements of ELC and ILC (arrow).

bursa. Spicule length 1.15–1.23 mm. Gubernaculum length 185–207. Dorsal ray length 392–448. Dermal collar well-developed on ventral surface of genital cone. Appendages of genital cone oval with finger-shaped projections. Protrusions of dermal collar present.

Female. Body length 9.9–11.2 mm. Esophagus length 745–812. BC width 101–149, depth 25–33. Anterior end to: deirids 487–588; excretory pore 512–666. Vulva to tail tip 252–336. Anus to tail tip 157–213. Vagina length 308–448. Egg size 80–84 × 40–44. Female tail straight.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

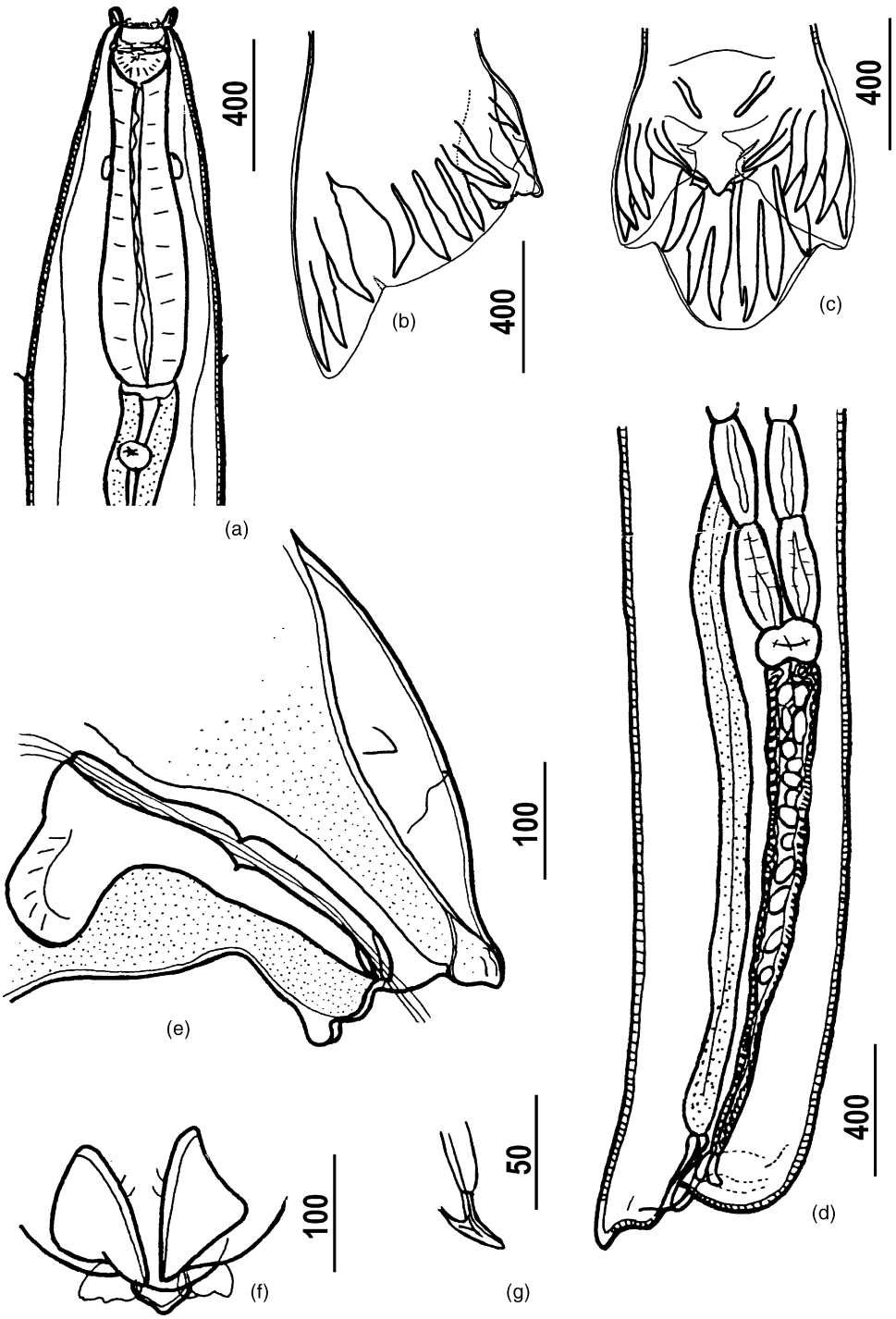

Fig. 85. *Cylicocyclus auriculatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (From Dvojnos and Kharchenko, 1994).

6.7.5. C. asini Matthee et al., 2002 (Figs. 83 and 84)

General. Dorsal and ventral notches on mouth collar present. Amphids project above MC surface. Tip of submedian papillae spindle-shaped, about four or more times as long as thick. ELC of 40–46 elements; longer than numerous ILC elements. Elements of ELC longer than broad. Tips of elements of ILC rounded. BC walls

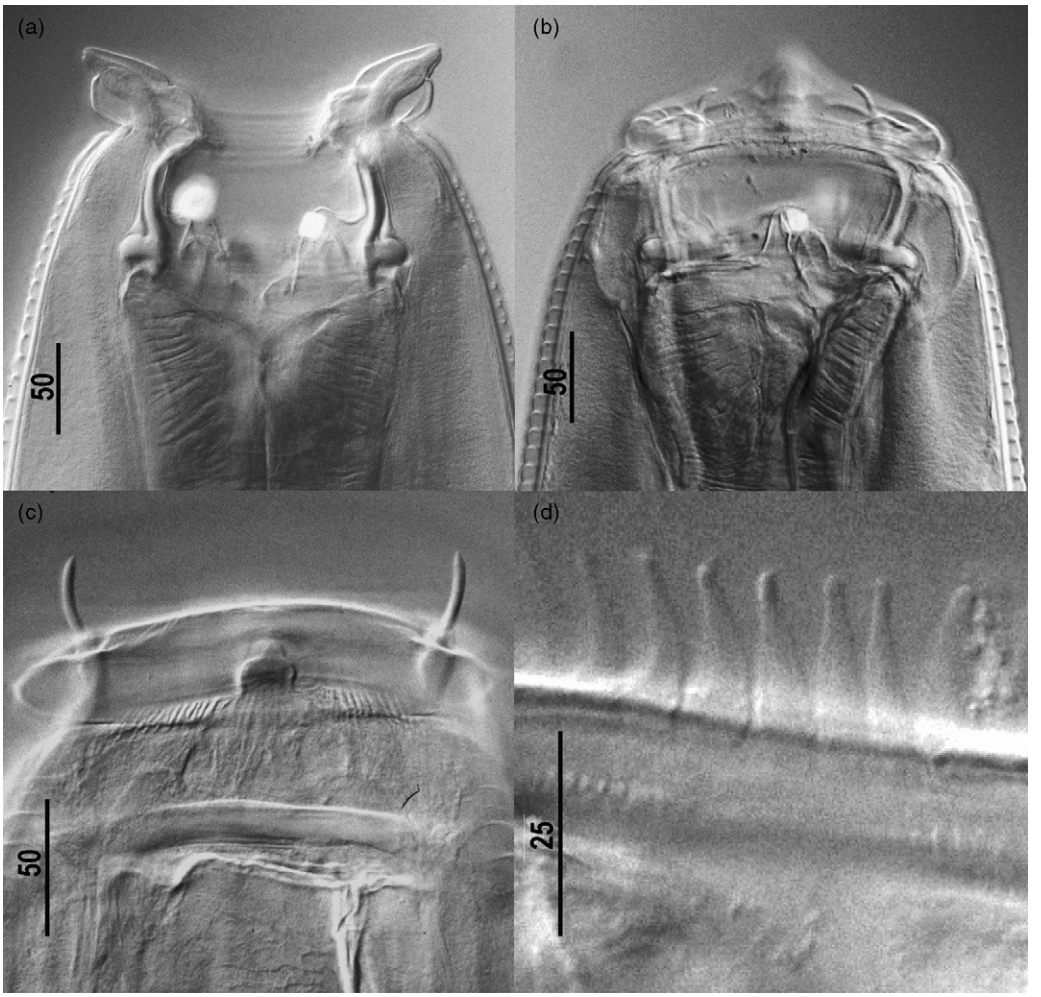

Fig. 86. *Cylicocyclus auriculatus.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Submedian papillae and elements of ILC. (d) Elements of ILC and ELC.

straight with posterior ring. Dorsal gutter button-like. Esophageal funnel shallow. Excretory pore posterior to NR. Deirids near middle of glandular esophagus. Esophageal–intestinal valve not elongated.

Male. Body length 5.25–6.90 mm. Esophagus length 0.90–1.0 mm. BC width 62–78, depth 28–38. Anterior end to: deirids 454–536; excretory pore 428–567. Male genital cone not covered by lateral lobes of bursa. Spicule length 2.32–2.88 mm. Gubernaculum length 221–265. Dorsal ray length 441–880. Externodorsal rays origin on stem of dorsal ray. Dermal collar not developed. One pair of appendages of genital cone nipple-like. Protrusions of dermal collar absent.

Female. Body length 7.18–8.97 mm. Esophagus length 0.88–1.12 mm. BC width 62–90, depth 25–40. Anterior end to: deirids 473–611; excretory pore 510–611. Vulva to tail tip 306–336. Anus to tail tip 64–160. Vagina length 528–848. Egg size 35–115 × 17–65. Tail club-shaped.

Hosts. *E. asinus*, *E. burchelli*, *E. zebra*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.7.6. *C. auriculatus (Looss, 1900) Chaves, 1930 (Figs. 85 and 86)*

Synonyms. *Cyathostomum auriculatum* Looss, 1900; *Cylichnostomum auriculatum* (Looss, 1900) Looss, 1902; *Cylicostomum auriculatum* (Looss, 1900) Gedoelst, 1903; *Trichonema auriculatum* (Looss, 1900) Le Roux, 1924.

General. Dorsal and ventral notches on mouth collar absent. Amphids extremely long, earlike or hornlike, extend much higher than mouth collar and submedian papillae. Tips of submedian papillae very long, uniform

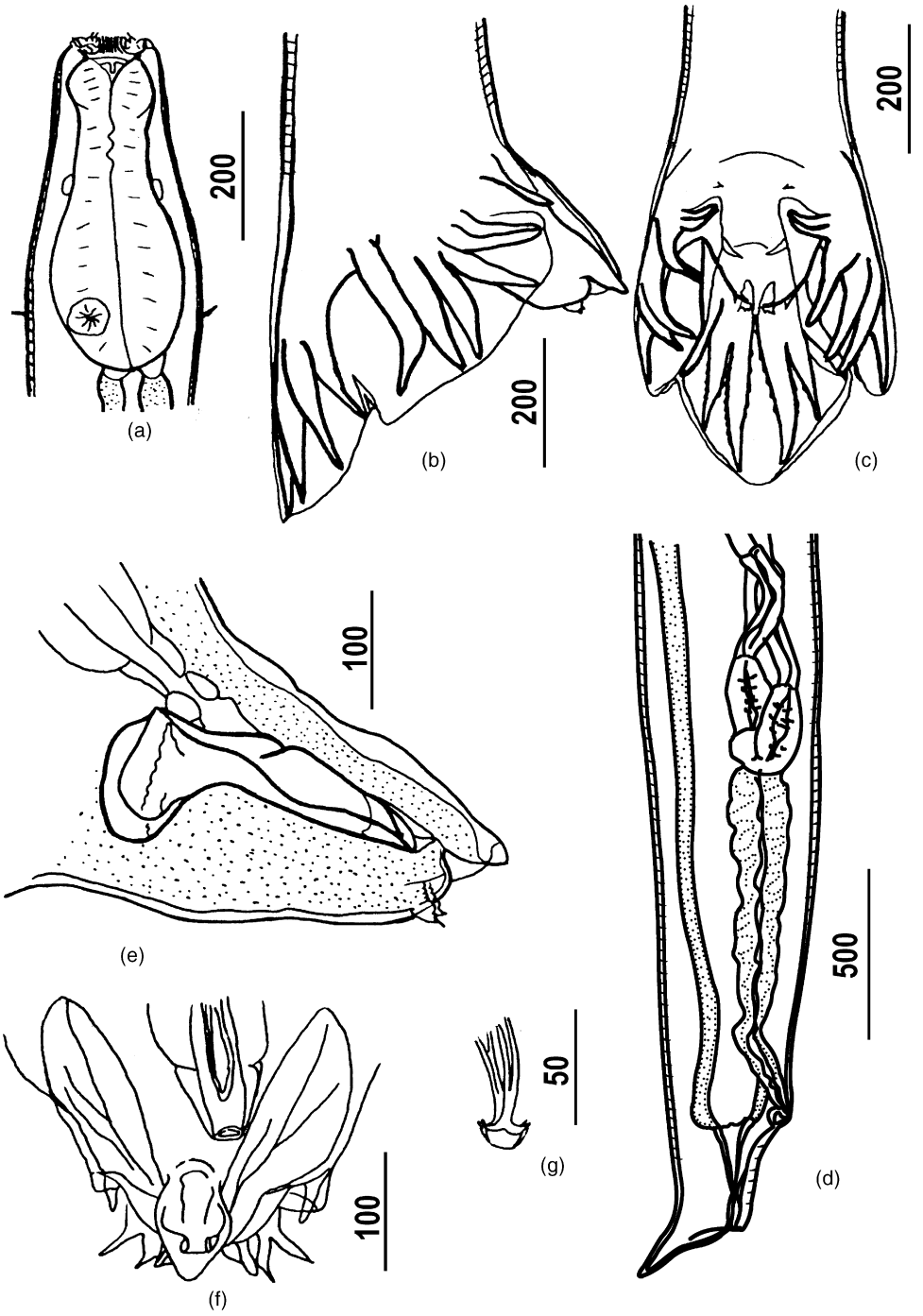

Fig. 87. *Cylicocyclus brevicapsulatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

thickness, about four or more times as long as thick. Stalk of submedian papillae shorter than broad. ELC of 42 elements; longer than numerous ILC elements. Elements of ELC longer than broad. Tips of elements of ILC pointed. BC walls straight with posterior ring. Dorsal gutter button-like. Esophageal funnel moderately enlarged. Excretory pore and deirids posterior to EI. Esophageal–intestinal valve not elongated.

Male. Body length 15–17 mm. Esophagus length 0.95–1.1 mm. BC width 137–160, depth 64–75. Spicule

length 1.80–2.17 mm. Gubernaculum length 323–341. Dorsal ray length 652–900. Ventral rays length equal to laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone oval with blunt end. Protrusions of dermal collar absent.

Female. Body length 26 mm. Esophagus length 1.15–1.28 mm. BC width 146–168, depth 72–78. Vulva to anus 130–190. Anus to tail tip 70–100. Vagina length 1.7–1.9 mm. Egg size 86–90 × 44–48. Tail of adult females curved dorsally at right angle.

Hosts. *Equus caballus*, *E. asinus*, *E. burchelli*, *E. zebra*.

Locality. Cecum, colon.

Distribution. Asia, Africa.

6.7.7. C. brevicapsulatus (Ihle, 1920) Ershov, 1930 (Figs. 87 and 88)

Synonyms. *Cylicostomum brevicapsulatum* Ihle, 1920; *Cylicobrachytus brevicapsulatum* (Ihle, 1920) Cram, 1924; *Trichonema brevicapsulatum* (Ihle, 1920) Mönnig, 1926.

General. Dorsal and ventral notches on MC absent. Amphids project above MC surface. Tips of submedian papillae bullet-shaped, two to three times as long as thick. Stalks of submedian papillae longer than broad. ELC markedly less numerous (42–48), and longer, than ILC (50–65). Elements of ELC longer than broad. Tips of ELC elements pointed. Tips of ILC elements rounded. BC walls very delicate, inconspicuous. Buccal cavity extremely shallow. Dorsal gutter not apparent.

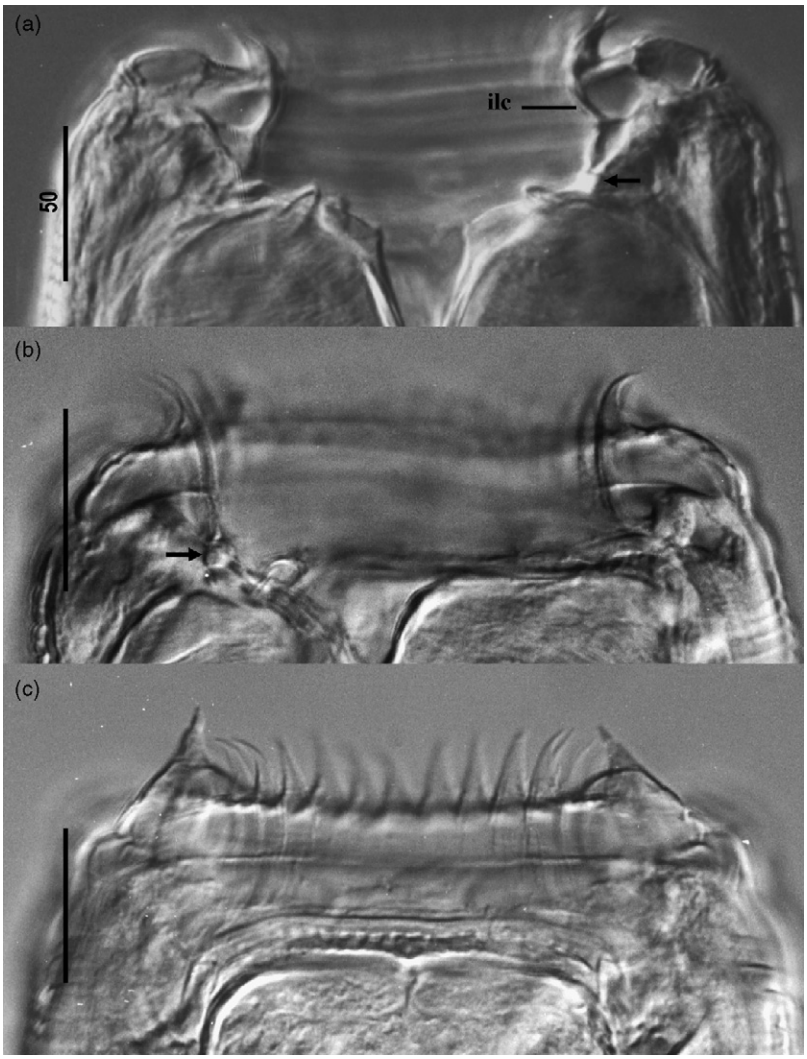

Fig. 88. *Cylicocyclus brevicapsulatus.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. Arrow marks ring at base of BC. (c) Submedian papillae and elements of ILC and ELC.

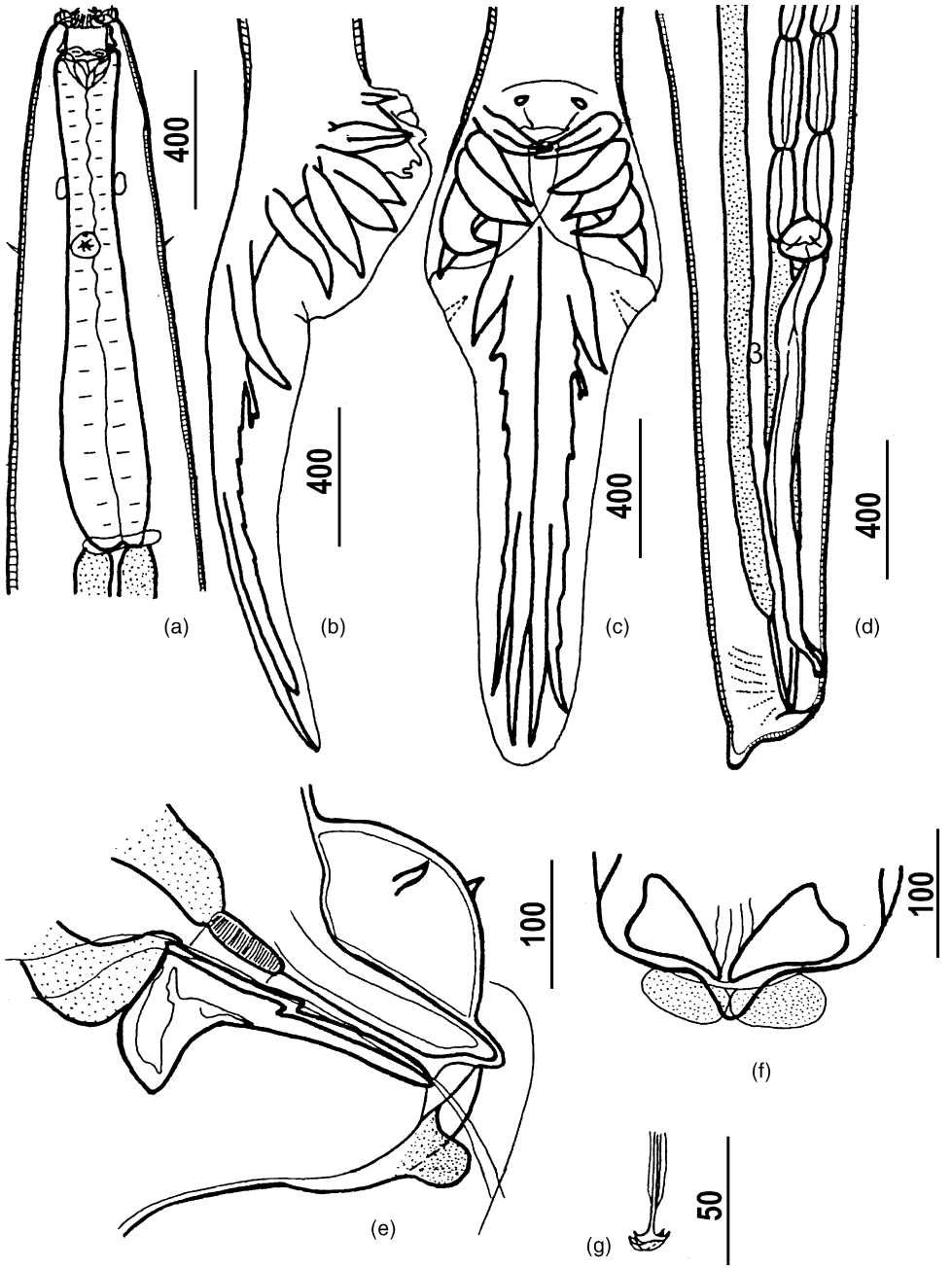

Fig. 89. *Cylicocyclus elongatus.* (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (from Dvojnos and Kharchenko, 1994).

Esophageal funnel shallow. Excretory pore posterior to NR. Deirids near middle of glandular esophagus. Esophageal–intestinal valve not elongated.

Male. Body length 9.0–11.5 mm. Esophagus length 450–540. BC width 81–130, depth 9–15. Anterior end to: deirids 353–412; excretory pore 341–434. Spicule length 1.74–1.97 mm. Gubernaculum length 210–270. Dorsal ray length 480–600. Ventral rays shorter than laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone finger-shaped, of variable length. Protrusions of dermal collar finger-shaped.

Female. Body length 10.0–13.9 mm. Esophagus length 550–635. BC width 106–139, depth 13–17.

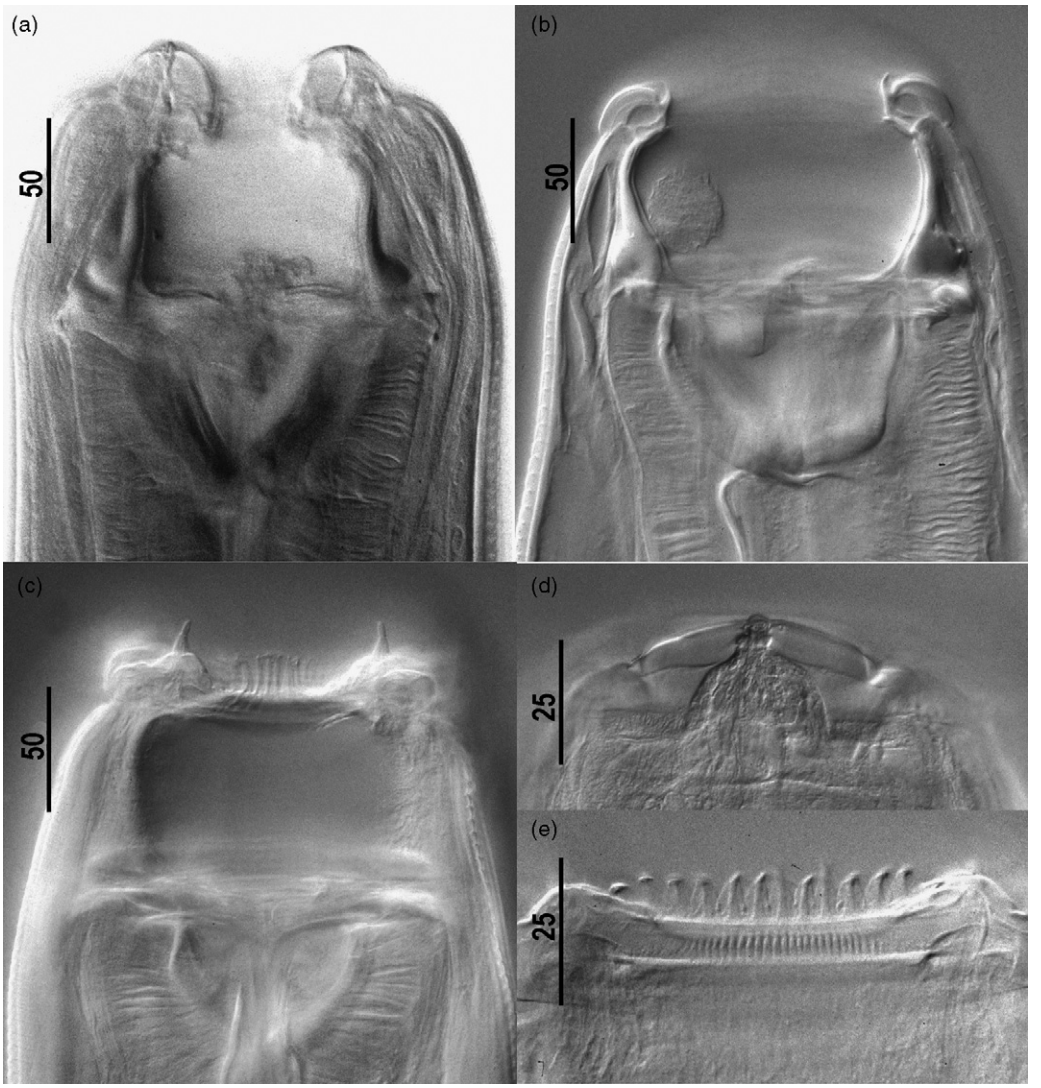

Fig. 90. *Cylicocyclus elongatus.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Submedian papillae and elements of ILC and ELC. (d) Lateral papilla. (e) Elements of ELC and ILC.

Anterior end to: deirids 466–690; excretory pore 417–542. Vulva to tail tip 480–740. Anus to tail tip 210–370. Egg size 85–90 × 47–50.

Hosts. *Equus caballus*, *E. asinus*.

Locality. Cecum, colon.

Distribution. Asia, Europe, North and South America.

6.7.8. C. elongatus (Looss, 1900) Chaves, 1930 (Figs. 89 and 90)

Synonyms. *Cyathostomum elongatum* Looss, 1900; *Cylichnostomum elongatum* (Looss, 1900) Looss, 1902; *Cylicostomum elongatum* (Looss, 1900) Gedoelst, 1903; *Trichonema elongatum* (Looss, 1900) Le Roux, 1924.

General. Amphids project slightly above MC surface. Tips of submedian papillae bullet-shaped, two to three times as long as thick. Stalks of submedian papillae longer than broad. ELC markedly less numerous (50–54), and longer, than ILC (84–86). Elements of ELC longer than broad. Tips of elements of ILC pointed. BC walls concave; posterior ring well-developed. Dorsal gutter not apparent. Esophageal funnel greatly enlarged, with thick cuticular lining. Excretory pore posterior to NR. Deirids near middle of glandular esophagus. Esophagus greatly elongated with posterior half enlarged but cylindrical. Esophageal–intestinal valve not elongated.

Male. Body length 12.2–16.2 mm. Esophagus length 1.42–1.44 mm. BC width 122–156, depth 63–97.

Spicule length 2.1–2.2 mm. Gubernaculum length 252–272. Dorsal ray length 1.65–1.9 mm. Ventral rays shorter than laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone oval.

Female. Body length 16–17 mm. Esophagus length 1.55 mm. BC width 178, depth 113. Vulva to anus 162. Anus to tail tip 243. Egg size 105–111 × 48–52.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.7.9. *C. gyalocephaloides* Ortlepp, 1938 (Figs. 91 and 92)

General. Amphids project slightly above MC surface. Tips of submedian papillae bullet-shaped, about two to three times as long as thick. Stalks of submedian papillae longer than broad. ELC elements markedly less numerous (38–44), and longer, than ILC elements

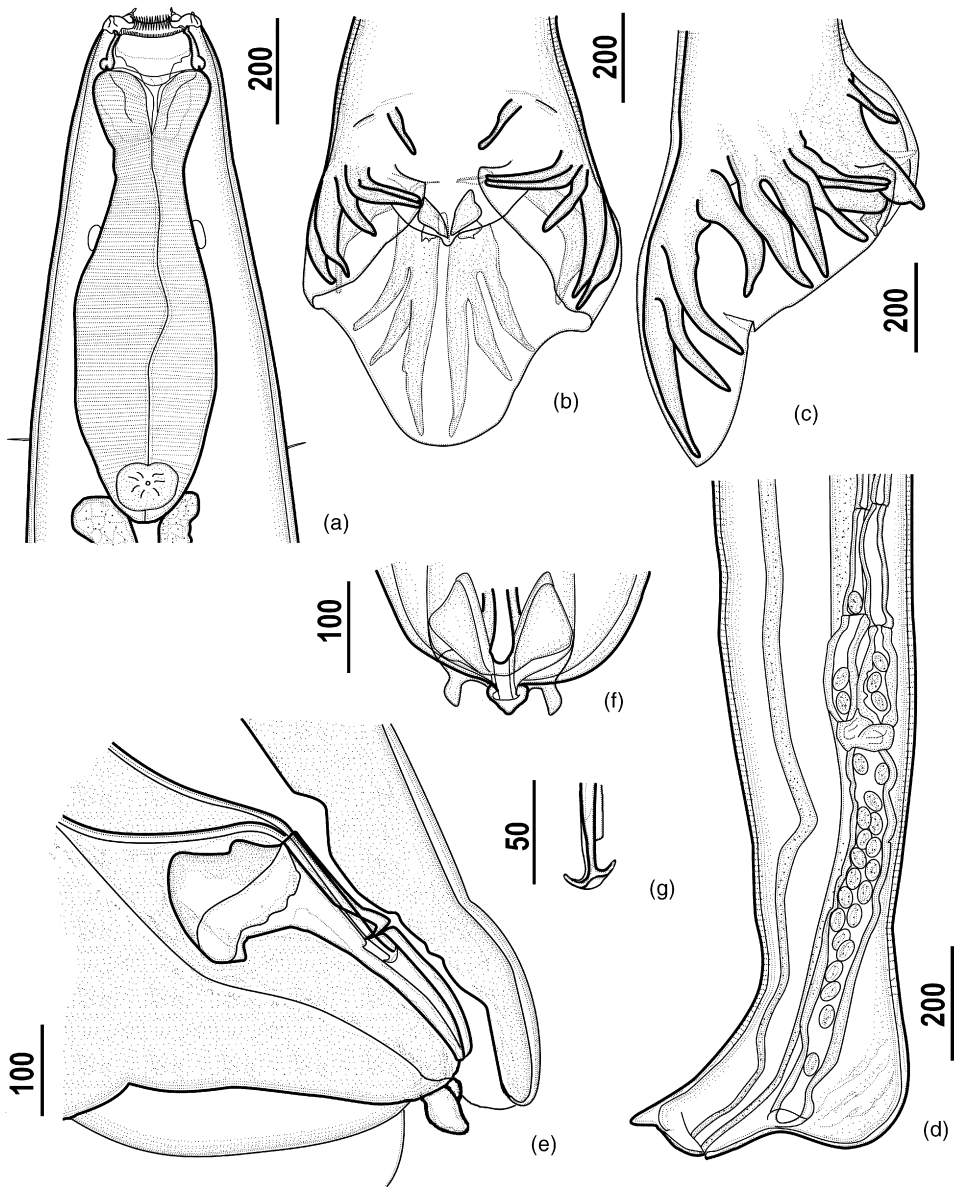

Fig. 91. *Cylicocyclus gyalocephaloides*. (a) Esophageal region, ventral view. (b) Male tail, ventral view. (c) Male tail, lateral view. (d) Male genital cone, ventral view. (e) Male genital cone and gubernaculum, lateral view. (f) Distal ends of spicules, ventral view, showing pick-like tips on each spicule. (g) Female tail, lateral view (from Lichtenfels et al., 2005).

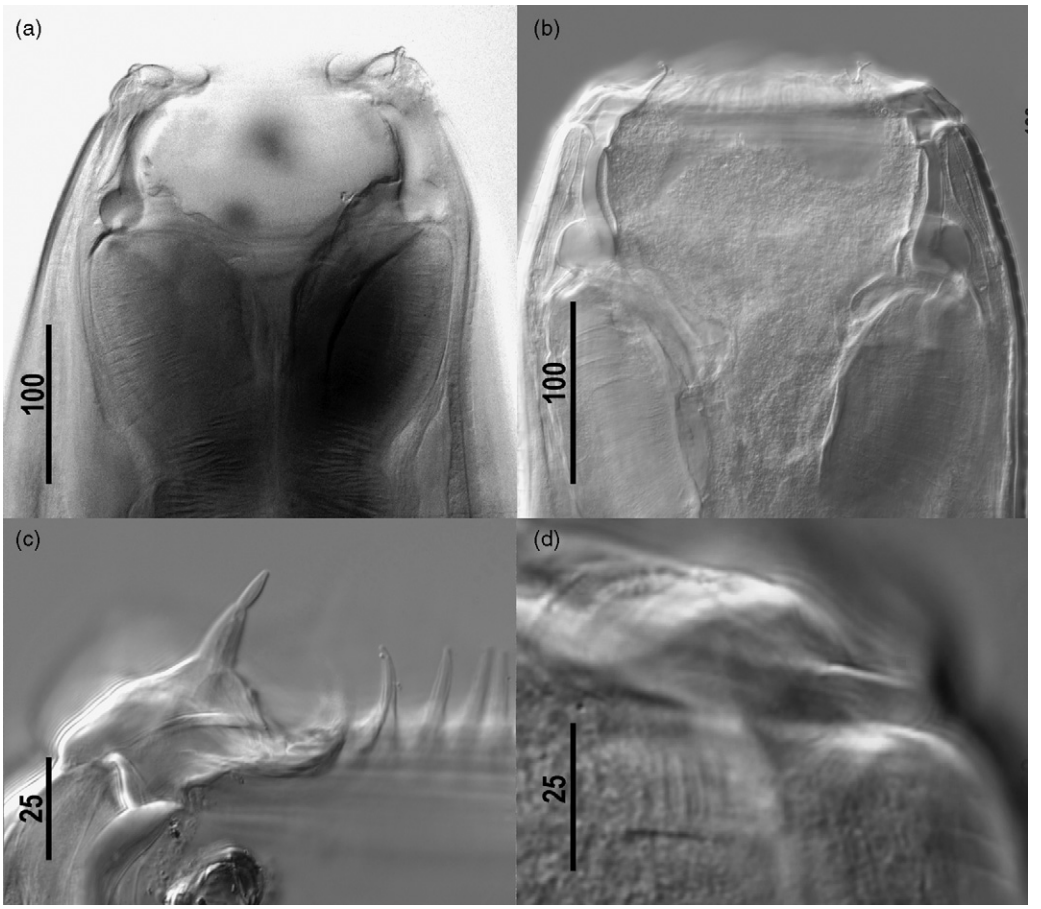

Fig. 92. *Cylicocyclus gyalocephaloides.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Submedian papilla and elements of ELC. (d) Elements of ILC.

(140–150). Elements of ELC longer than broad. Tips of elements of ILC pointed. BC walls concave; posterior ring well-developed. Dorsal gutter not apparent. Esophageal funnel greatly enlarged, without thick cuticular lining. Excretory pore and deirids near EI. Esophageal–intestinal valve not elongated.

Male. Body length 9.0–14.0 mm. Esophagus length 0.82–1.06 mm. BC width 195–224, depth 68–98. Spicule length 2.1–2.6 mm. Gubernaculum length 293–371. Dorsal ray length 586–1001. Ventral rays length equal to laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone well-developed cylindrical, with nipples on the both sides, but more slender then in *C. insigne* and lacking lateral spines.

Female. Body length 6.5–16.0 mm. Esophagus length 0.89–1.20 mm. BC width 146–254, depth 68–107. Vulva to tail tip 283–537. Anus to tail tip 122–244. Egg size 79–110 × 49–61. Tail club-shaped.

Hosts. *E. burchelli*.

Locality. Cecum, colon.

Distribution. Africa.

6.7.10. C. insigne (Boulenger, 1917) Chaves, 1930 (Figs. 93 and 94)

Synonyms. *Cylichnostomum insigne* Boulenger, 1917; *Cylicostomum insigne* (Boulenger, 1917) Ransom and Hadween, 1918; *Trichonema insigne* (Boulenger, 1917) Le Roux, 1924; *Trichonema insigne rosenbuschi* Galofré and Rosa, 1944.

General. Amphids project slightly above MC surface. Tips of submedian papillae bullet-shaped, about two to three times as long as thick. Stalks of submedian papillae longer than broad. ELC elements markedly less numerous (38–44), and longer, than ILC elements (140–150). Elements of ELC longer than broad. Tips of elements of ILC pointed. BC walls concave; posterior ring well-developed. Dorsal gutter not apparent. Esophageal funnel greatly enlarged, without thick cuticular lining. Excretory pore and deirids near EI. Esophageal–intestinal valve not elongated.

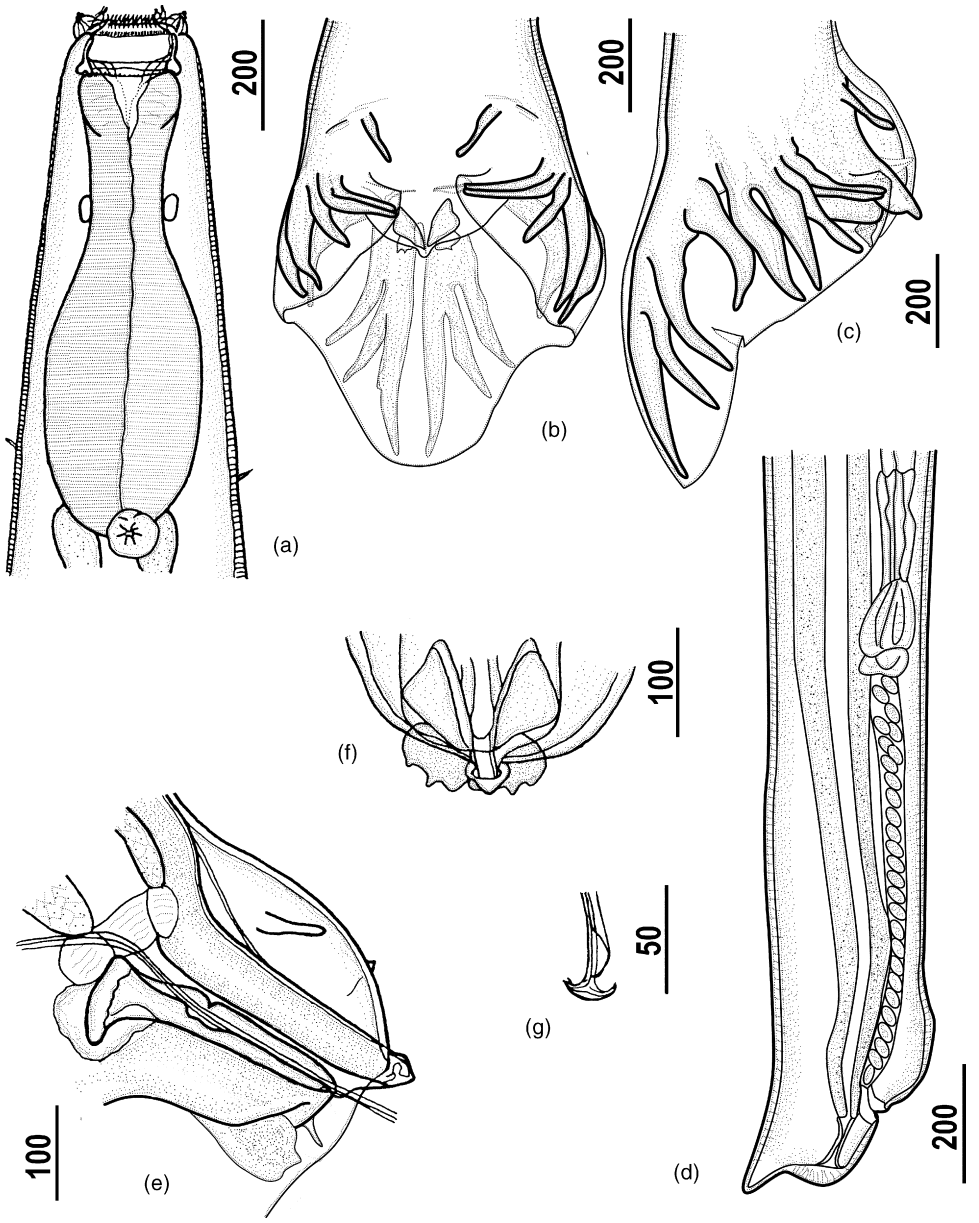

Fig. 93. *Cylicocyclus insigne.* (a) Esophageal region, ventral view. (b) Male tail, ventral view. (c) Male tail, lateral view. (d) Male genital cone, ventral view. (e) Male genital cone and gubernaculum, lateral view. (f) Distal ends of spicules, ventral view, showing pick-like tips on each spicule. (g) Female tail, lateral view (from Lichtenfels et al., 2005).

Male. Body length 9.5–13.0 mm. Esophagus length 700–900. BC width 135–197, depth 46–66. Spicule length 3.00–3.56 mm. Gubernaculum length 268–284. Dorsal ray length 700–730. Ventral rays length equal to laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone well-developed, cylindrical, with spines on the both sides.

Female. Body length 12.6–17.1 mm. Esophagus length 820. BC width 130–200, depth 56–72. Vulva to tail tip 280–480. Anus to tail tip 160– 250. Egg size 88–94 × 54–56.

Hosts. Equus caballus, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

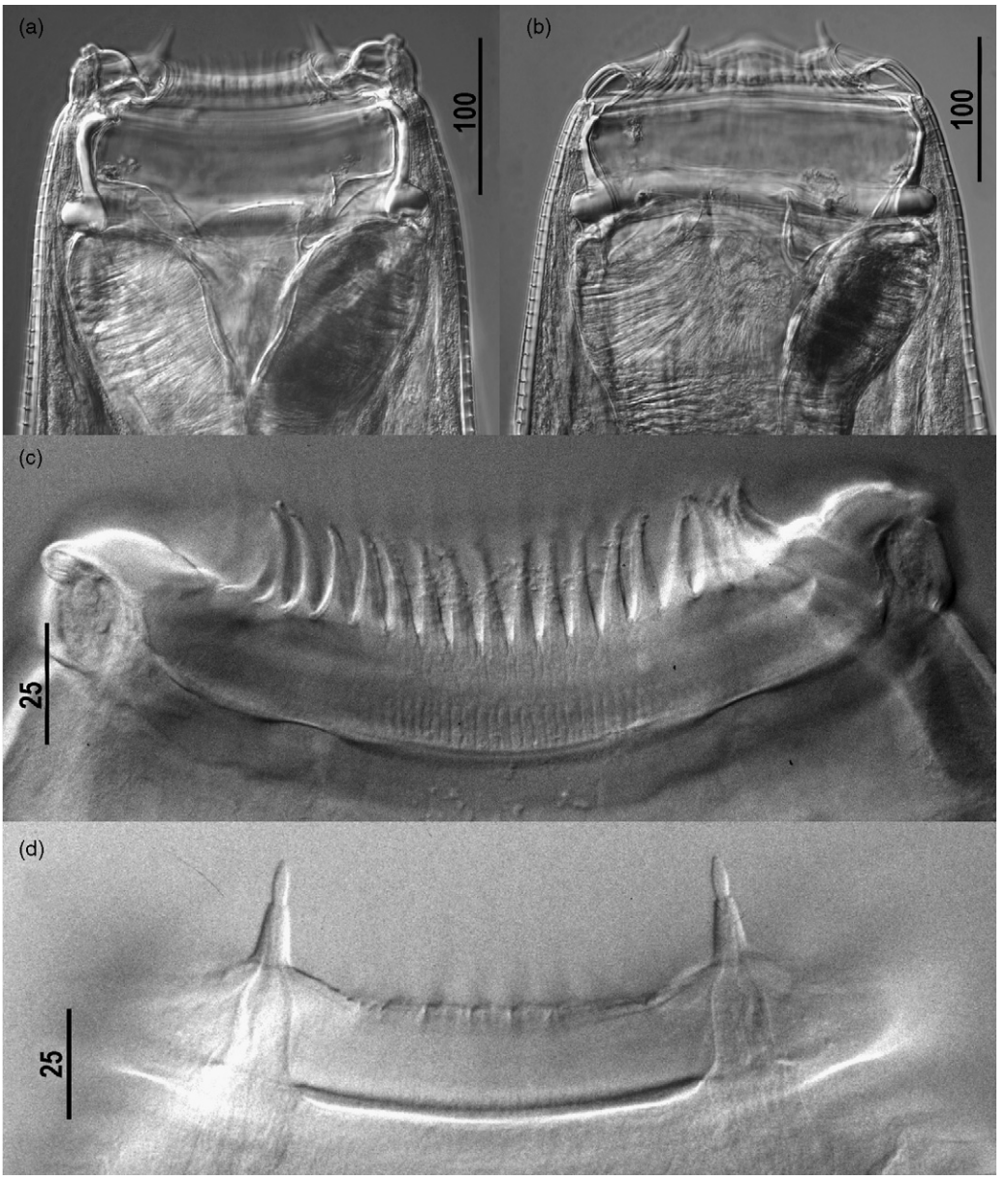

Fig. 94. *Cylicocyclus insigne.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Elements of ILC and ELC. (d) Submedian papillae.

6.7.11. C. leptostomum Kotlán, 1920 (Figs. 95 and 96)

Synonyms. *Cylicostomum leptostomum* Kotlán, 1920; *Trichonema leptostomum* (Kotlán, 1920) Le Roux, 1924; *Schulzitrichonema leptostomum* (Kotlán, 1920) Ershov, 1943; *Cylicotetrapedon leptostomum* (Kotlán, 1920) K'ung, 1964; *Cyathostomum bogoriense* Smit and Notosoediro, 1923.

General. Amphids project above MC surface. Tips of submedian papillae bullet-shaped, two to three times as long as thick. Stalks of submedian papillae longer than broad. ELC markedly less numerous (20–24), and longer, than ILC (50–60). Elements of ELC longer than broad. Tips of elements of ILC rounded. BC walls thicken gradually toward base without marked offset of ring. Buccal cavity cylindrical. Dorsal gutter button-like but distinct. Esophageal funnel small, with thin cuticular lining. Excretory pore posterior to NR. Deirids near middle of glandular esophagus. Esophageal–intestinal valve elongated.

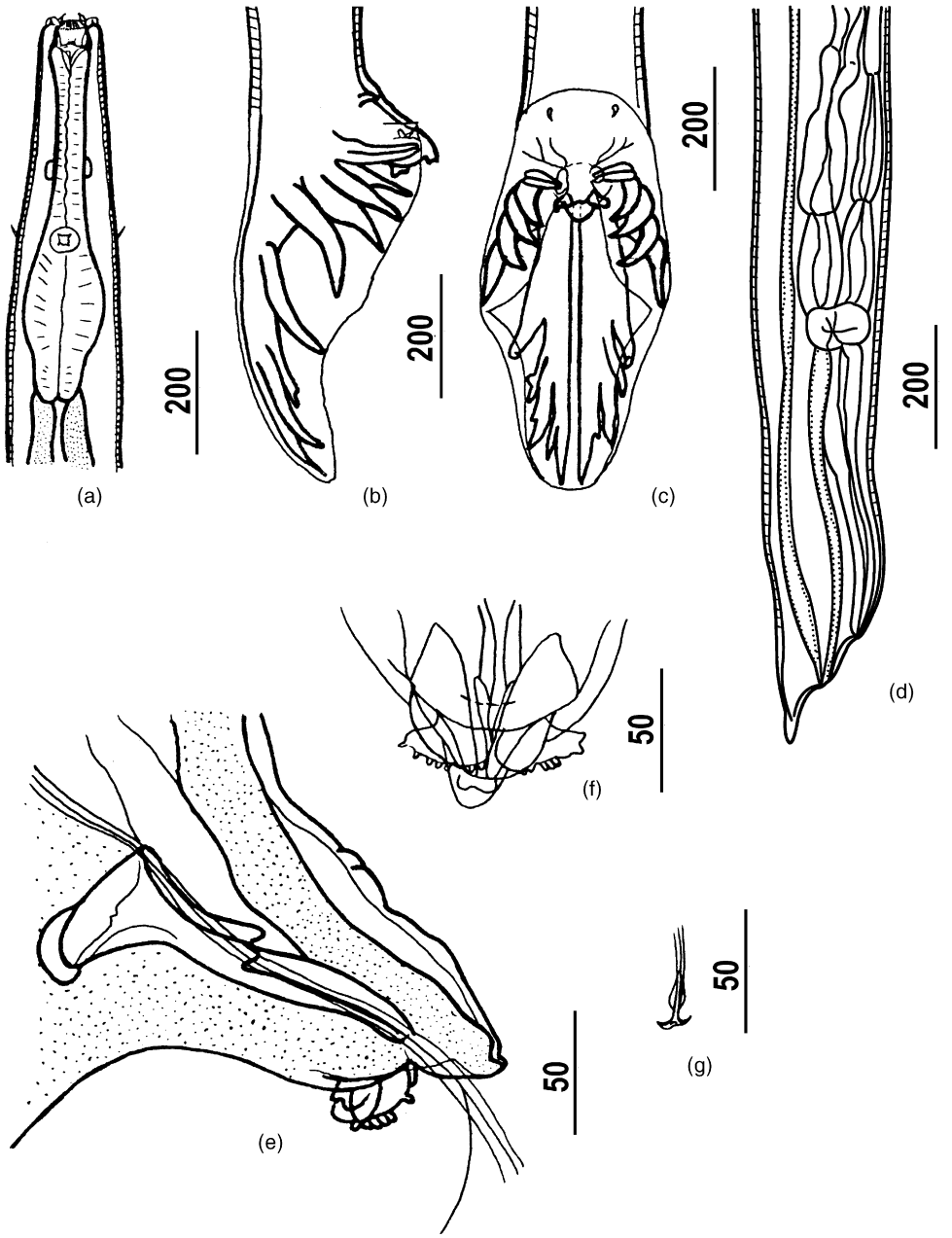

Fig. 95. *Cylicocyclus leptostomum.* (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

Male. Body length 5.9–6.3 mm. Esophagus length 480–548. BC width 40–44, depth 20–32. Spicule length 1.0–1.2 mm. Gubernaculum length 140–168. Dorsal ray length 360–440. Ventral rays length equal to laterals. Bursa edge smooth. Genital cone projects slightly from bursa. Dermal collar poorly developed on ventral side of genital cone. Appendages of genital cone oval with numerous finger-shaped projections

Female. Body length 6–8 mm. Esophagus length 520–650. BC width 44–60, depth 20– 24. Vulva to tail tip 220–304. Anus to tail tip 100–156. Egg size 58–100 × 38–40.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

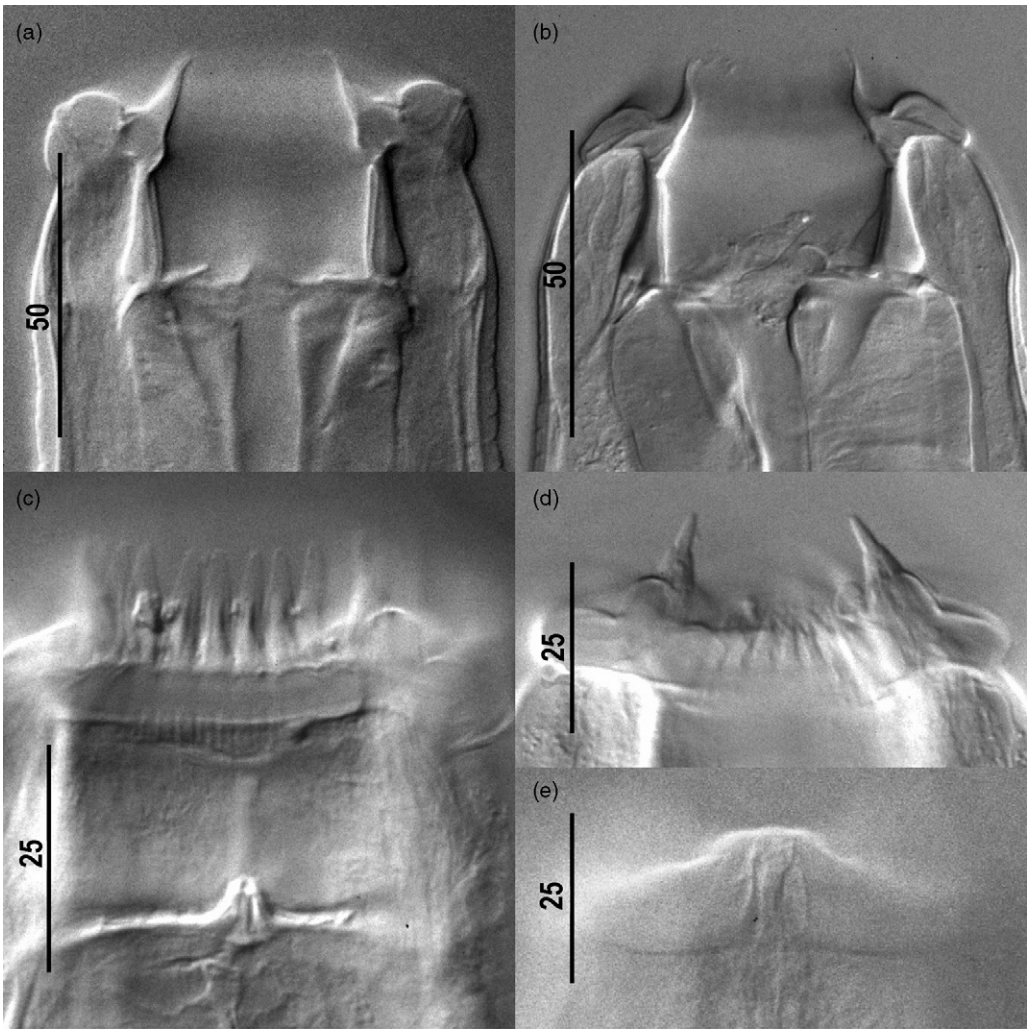

Fig. 96. *Cylicocyclus leptostomum.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Elements of ILC and ELC and triangular dorsal gutter. (d) Submedian papillae. (e) Lateral papilla.

6.7.12. C. nassatus (Looss, 1900) Chaves, 1930 (Figs. 97 and 98)

Synonyms. *Cyathostomum nassatum* Looss, 1900; *Cylichnostomum nassatum* (Looss, 1900) Looss, 1902; *Cylicostomum nassatum* (Looss, 1900) Gedoelst, 1903; *Trichonema nassatum* (Looss, 1900) Le Roux, 1924; *Cylicocyclus bulbiferus* Chaves, 1930.

General. Amphids project above MC surface. Tips of submedian papillae spindle-shaped, about four times as long as thick. Stalks of submedian papillae shorter than broad. ELC markedly less numerous (19–20), and longer, than ILC (56–62). Elements of ELC longer than broad. Tips of elements of ILC rounded. BC walls straight; posterior ring offset. Buccal cavity cylindrical. Dorsal gutter extends one-half depth of buccal cavity. Cuticular lining of BC with internal shelf-like projection Esophageal funnel shallow. Excretory pore posterior to NR. Deirids near middle of glandular esophagus. Esophageal–intestinal valve not elongated.

Male. Body length 7.4–8.3 mm. Esophagus length 594–678. BC width 70–111, depth 30–38. Spicule length 1.15–1.27 mm. Gubernaculum length 156–189. Dorsal ray length 403–448. Ventral rays length equal to laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone large, oval with several short nipple-shaped projections, sometimes fused medially.

Female. Body length 8.0–10.5 mm. Esophagus length 672–728. BC width 108–165, depth 32–42. Vulva to tail tip 319–392. Anus to tail tip 190–274. Egg size 87–95 × 40–48. Tail of mature female straight, tip slightly curved dorsally.

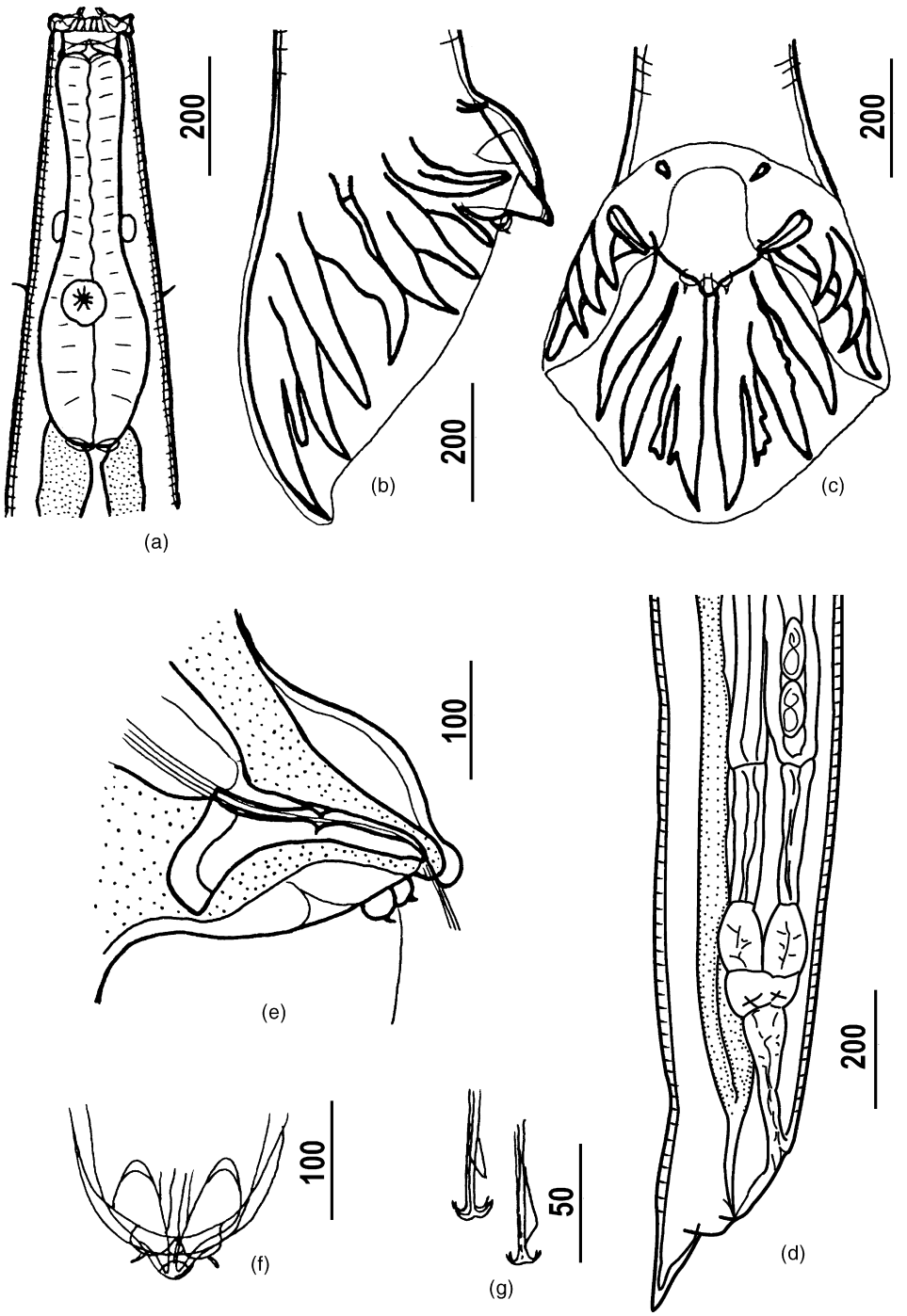

Fig. 97. *Cylicocyclus nassatus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Two variations of fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

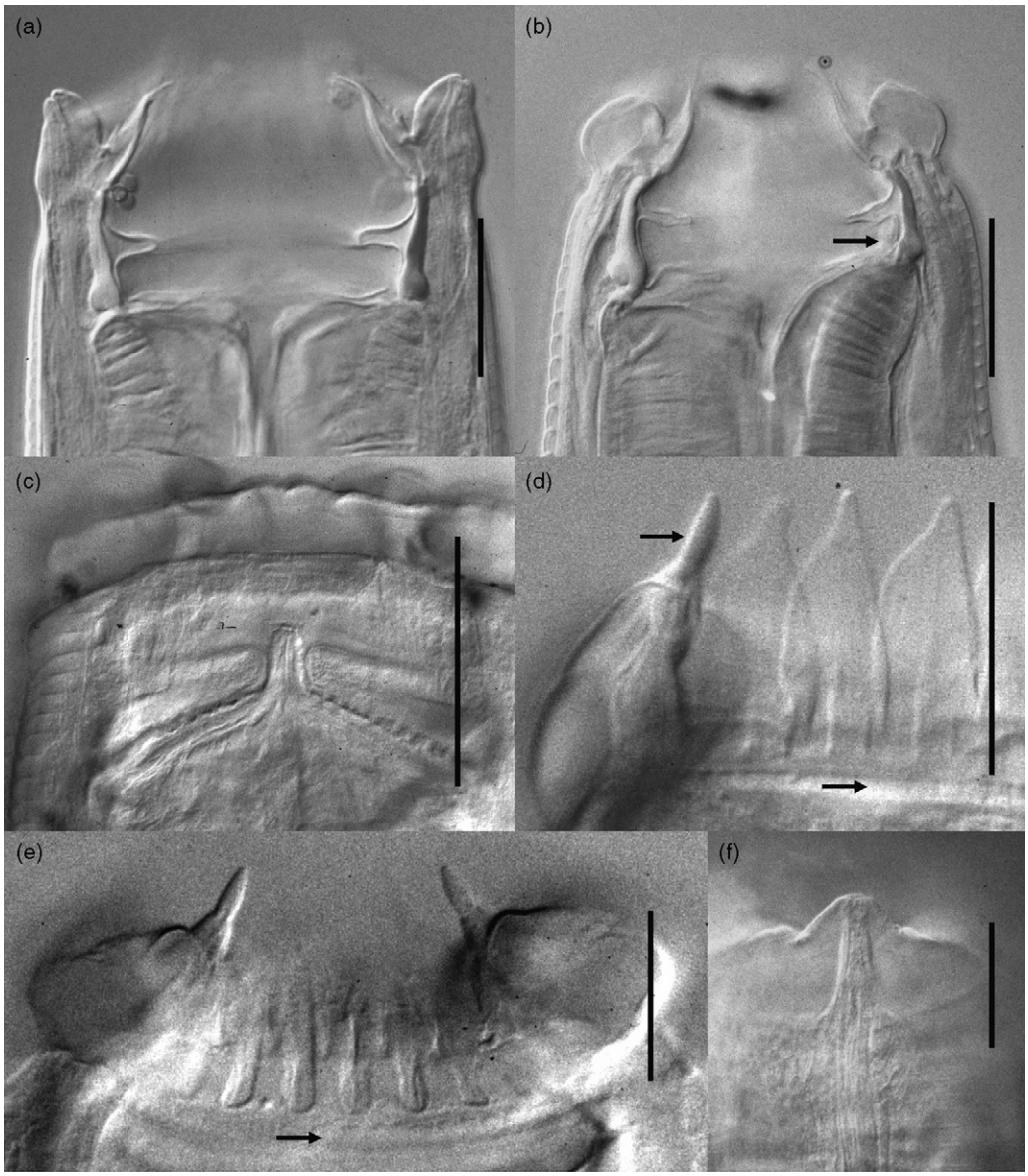

Fig. 98. *Cylicocyclus nassatus.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. Arrow marks dorsal gutter. (c) Dorsal gutter and cuticular shelf of lining of BC. (d) Submedian papillae and elements of ELC and ILC (arrow). (e) Submedian papillae and elements of ILC (arrow). (f) Lateral papilla.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.7.13. *C. triramosus (Yorke and Macfie, 1920) Chaves, 1930 (Figs. 99 and 100)*

Synonyms. *Cylicostomum triramosum* Yorke and Macfie, 1920; *Trichonema triramosum* (Yorke and Macfie, 1920) Le Roux, 1924.

General. Dorsal and ventral notches on mouth collar present. Amphids project above MC surface. Tips of submedian papillae spindle-shaped, about three times as long as thick. Stalks of submedian papillae shorter than broad. ELC and ILC each with 30 elements. Elements of ELC longer than broad and longer than ILC. Tips of elements of ILC rounded. BC walls concave; posterior ring offset. Dorsal gutter button-like. Esophageal funnel small, with thin cuticular lining. Excretory pore posterior to NR. Deirids near

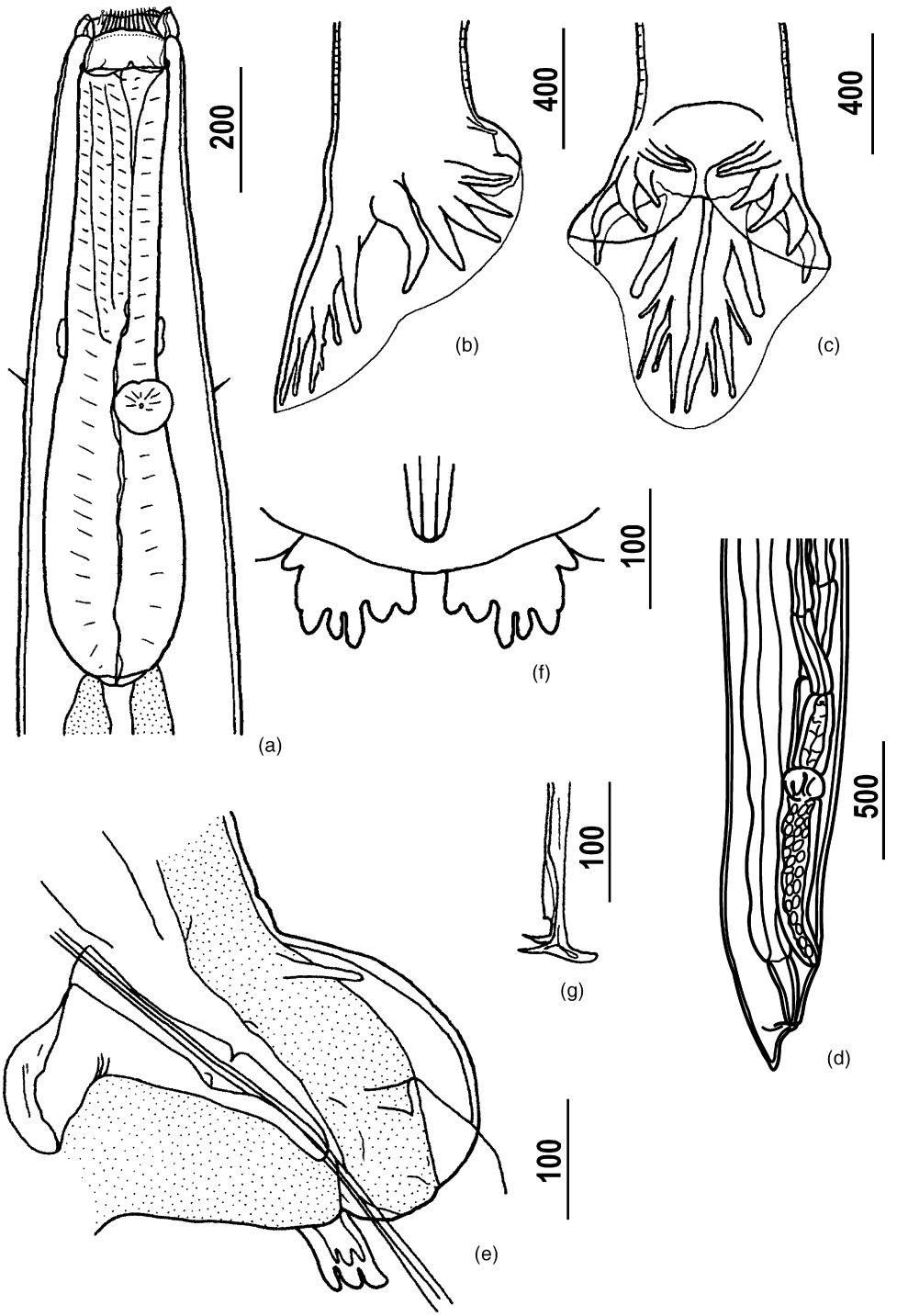

Fig. 99. *Cylicocyclus triramosus.* (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Kharchenko et al., 1997).

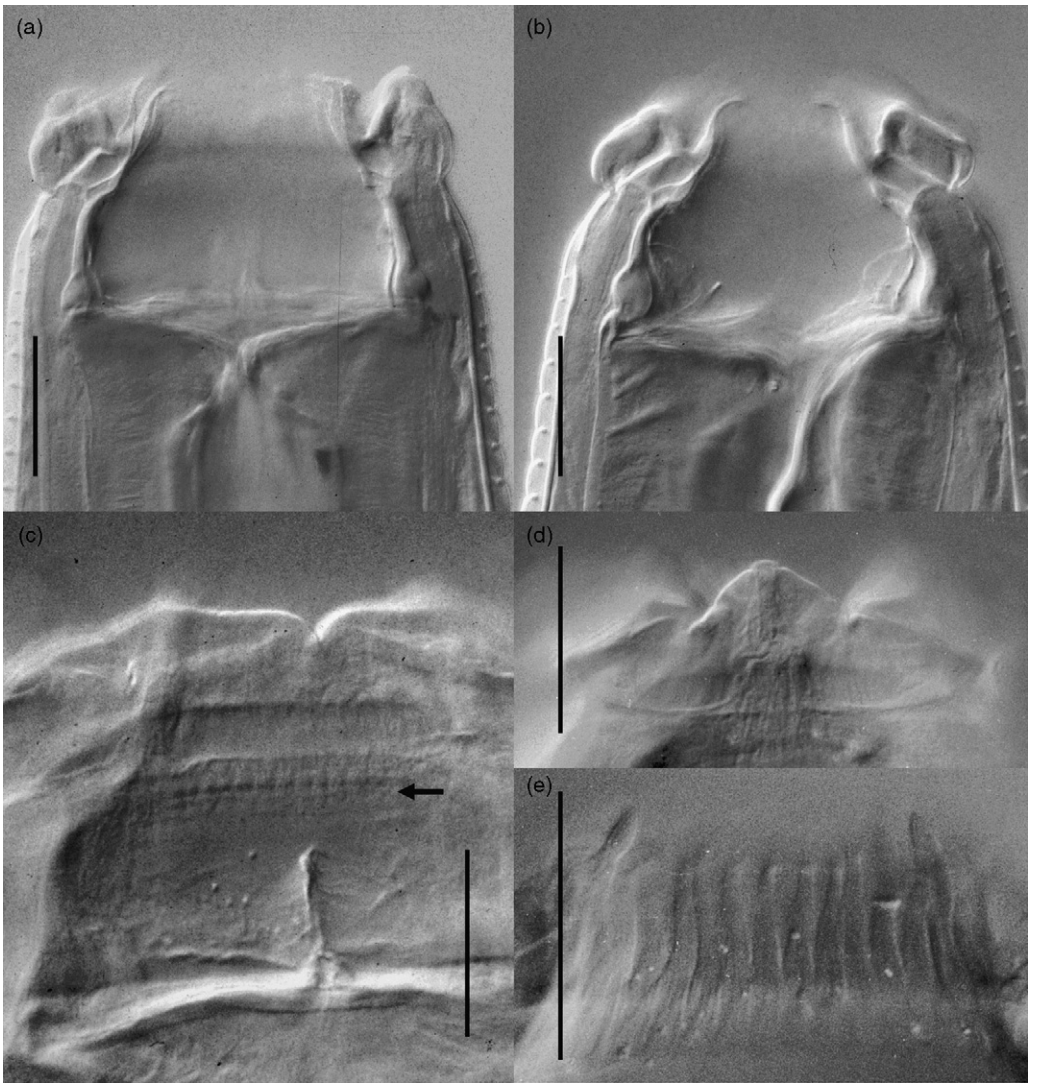

Fig. 100. *Cylicocyclus triramosus.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Elements of ILC (arrow) and dorsal gutter. (d) Lateral papilla. (e) Submedian papillae and elements of ELC (modified from Kharchenko et al., 1997).

middle of glandular esophagus. Esophageal–intestinal valve not elongated.

Male. Body length 7.8–11.3 mm. Esophagus length 0.75–1.12 mm. BC width 60–120, depth 22–50. Spicule length 2.20–2.97 mm. Gubernaculum length 204–278. Dorsal ray length 525–827. Ventral rays length equal to laterals. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone paired semilunar plates with finger-shaped processes on distal margin. Protrusions of dermal collar absent.

Female. Body length 11.6–14.2 mm. Esophagus length 0.96–1.19 mm. BC width 83–154, depth 34–50. Vulva to tail tip 529–654. Anus to tail tip 176–232. Egg size 54–82 × 38–46.

Hosts. *Equus burchelli antiquorum*, *E. zebra hartmannae*.

Locality. Cecum, colon.

Distribution. Africa.

6.7.14. C. ultrajectinus (Ihle, 1920) Ershov, 1939 (Figs. 101 and 102)

Synonyms. *Cylicostomum ultrajectinum* Ihle, 1920; *Trichonema ultrajectinum* (Ihle, 1920) Le Roux, 1924; *Cylicodontophorus ultrajectinum* (Ihle, 1920) Cram, 1924.

General. Posterior edge of MC at anterior edge of BC. Amphids do not project above MC surface. Tips of submedian papillae bullet-shaped, oval and short. Stalks

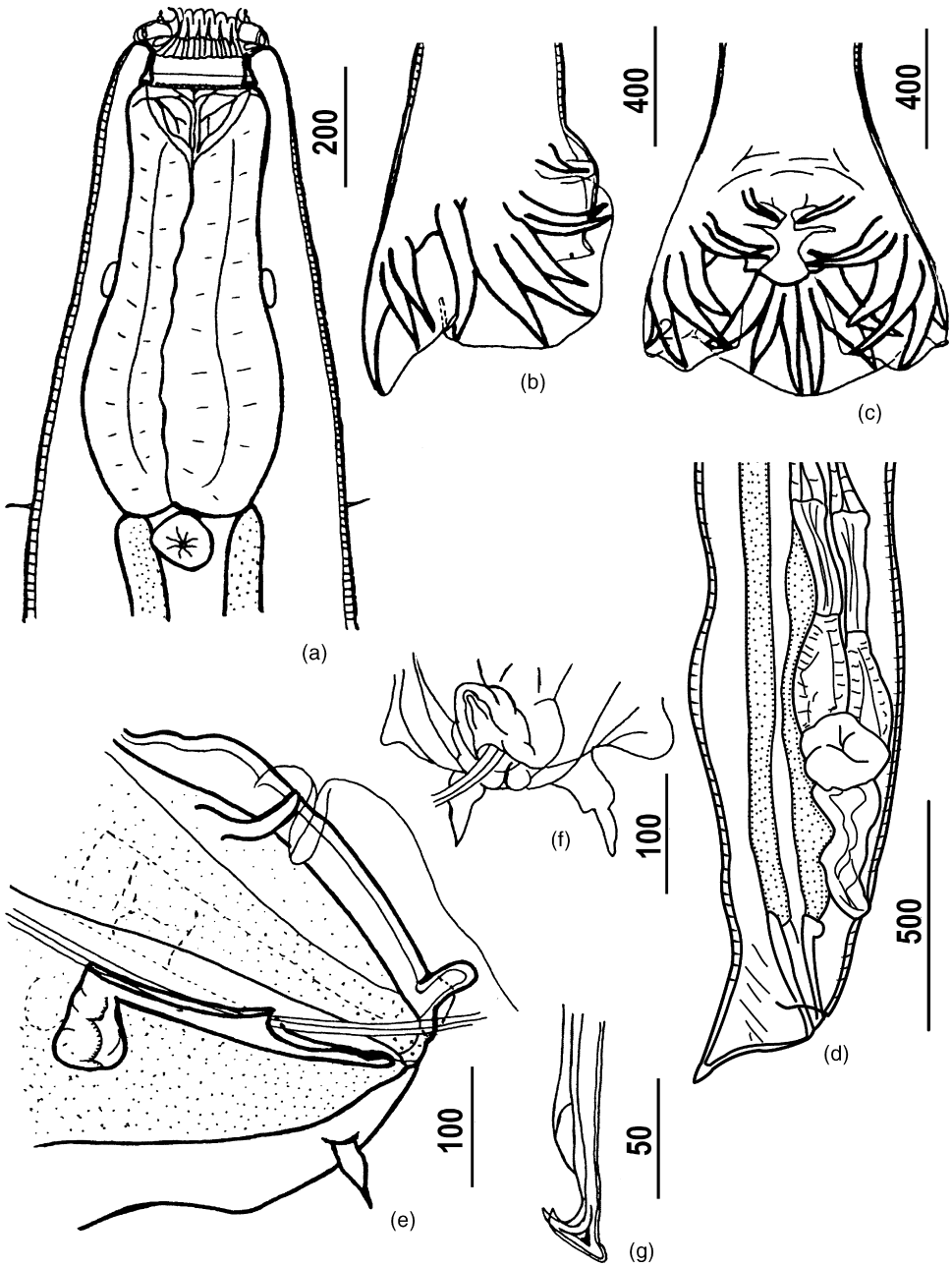

Fig. 101. *Cylicocyclus ultrajectinus.* (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Kharchenko et al., 1997).

of submedian papillae longer than broad. ELC markedly less numerous (10–12), and shorter, than ILC (46; 10–12 longer than others). Elements of ELC as long as broad, tips rounded. Tips of elements of ILC pointed. Insertion point for posterior ends of elements of ILC at $^1/_4$ or less of BC depth. BC walls concave with well developed posterior ring. Buccal cavity cylindrical. Dorsal gutter not apparent. Esophageal funnel enlarged. Excretory pore and deirids posterior to EI. Esophageal–intestinal valve not elongated.

Male. Body length 11–15 mm. Esophagus length 620–750. BC width 143–190, depth 55–63. Spicule length 1.75 mm. Gubernaculum length 273. Dorsal ray length 620–650. Ventral rays length equal to laterals.

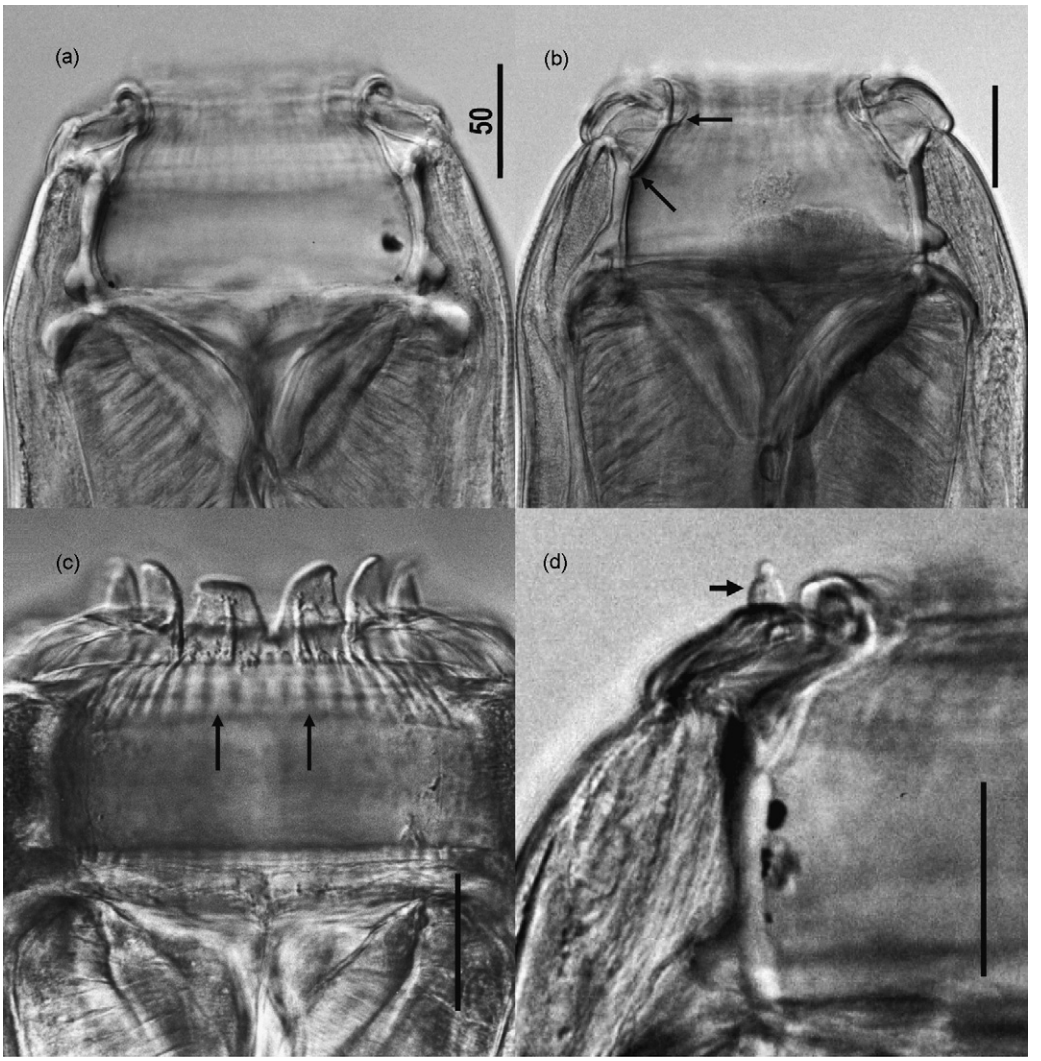

Fig. 102. *Cylicocyclus ultrajectinus.* (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. Arrows mark element of ILC. (c) Elements of ILC and ELC. Arrows mark longer ILC elements. (d) Submedian papilla (arrow), elements of ELC and ILC and BC wall.

Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone long sometimes bifurcated distally.

Female. Body length 11–19 mm. Esophagus length 770–800. BC width 143–190, depth 55–63. Vagina length 500. Vulva to tail tip 435–650. Anus to tail tip 170–270. Egg size 130–140 × 59–65.

Hosts. *Equus caballus*, *E. asinus*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.7.15. Discussion

The name *Cylicocyclus*, calling attention to the hoop-like thickening at the base of the buccal capsule, was proposed by Ihle (1922) as a subgenus. Cram (1925) elevated the group to generic level. There has been general agreement (Lichtenfels, 1975; Hartwich, 1986; Dvojnos and Kharchenko, 1994; Lichtenfels et al., 1998; Zhang and K'ung, 2002) concerning the relationship of most of the species presently included in this genus. Zhang and K'ung (2002) recognized *C. zhidanensis* Zang and Li, 1981; a species that we believe to be a synonym of *C. ashworthi*.

According to the molecular analysis of Hung et al. (2000), *C. ultrajectinus* differs from other members of this genus. However, until a morphological phylogeny of this genus is completed, we prefer to group *C. ultrajectinus* with the species of *Cylicocyclus*.

Hartwich (1986) correctly pointed out that *C. leptostomum* should retain the original nominative singular noun ending "*um*".

The question of whether *C. elongatus elongatus* and *C. elongatus kotlani* differ sufficiently to be recognized as separate species was raised by Lichtenfels (1975) and Lichtenfels et al. (1998). The available specimens of *C. elongatus* sensu lato, except the paratypes, are all *C. elongatus kotlani* (Ihle, 1920). This subspecies were described as a variety with a greatly elongated bursa (1.5 mm compared with 700 um for *C. elongatus elongatus*). Georgi and Whitlock (1971) also reported *C. elongatus kotlani* from New York. Baruš (1962) and Braide and Georgi (1974) reported *C. elongatus kotlani* to have 52–57 elements in the ELC rather than 36 as found in *C. elongatus elongatus* by Looss (1902). This difference in number of ELC elements was also reported by Popova (1958). Lichtenfels (1975) was able to confirm these differences between *C. e. elongatus* and *C. e. kotlani* by studying paratypes of the former which Looss deposited in the USNM Helminthological Collection. In addition he observed the vagina of *C. e. elongatus* females to be significantly shorter than that of *C. e. kotlani*. These differences between the two subspecies are as great as those between many species and further study may provide convincing evidence that they are separate species. For the present, because males of *C. elongatus elongatus* are not available, we prefer to retain the subspecies designations.

Cylicocyclus ashworthi was redescribed by Lichtenfels et al. (1997). Hartwich (1986) and others had considered this species to be a synonym of *C. triramosus*, but Kharchenko et al. (1997) redescribed *C. triramosus*, which is restricted to zebras, and differentiated the two species. The species *C. triramosus* was described from one male and one female from zebra from Namibia (Yorke and Macfie, 1920). The description was extended by Theiler (1924), who added three specimens from two zebras. These descriptions were repeated exactly in a number of monographs (Ihle, 1922; Skrjabin and Ershov, 1933 in Popova, 1958). Nobody disputed the validity of *C. triramosus*. The confusion arose after *C. ashworthi* Le Roux (1924) was described and Ihle (1925) synonimized it with *C. nassatus*. Some authors around the world, particulary in Russian language helminthological literature (Ivashkin and Dvojnos, 1984; Ershov, 1933; Mendelevich, 1940 and others), distinguished, in their own material, two species; and, since they considered *C. ashworthi* to be identical to *C. nassatus*, they identified (incorectly) *C. ashworthi* as *C. triramosus*. This resulted in Hartwich (1986) synonimizing *C. ashworthi* with *C. triramosus*. The study of helminths of zebra conducted by R. Krecek in South Africa (Scialdo-Krecek, 1984) confirmed, that in spite of cosmopolity of the overwelming majority of species of cyathostomins, some are restricted to zebras. Kharchenko et al. (1997) determined that *C. triramosus* is parasitic only in zebra and has been found only in Southern Africa. This species is similar to *C. ashworthi, C. nassatus, C. leptostomum* and *C. radiatus*. It is most similar to the latter (redescribed by Lichtenfels et al., 1998), particularly with the thin buccal walls, with a large hoop-shaped thickening.

Recently a new species, *C. asini* parasitic in *E. asinus* in Africa, was added to this genus (Matthee et al., 2002). This species is similar to *C. triramosus*, but differs in shape of both male and female tails as well as other characteristics.

Cylicocyclus adersi (Boulenger, 1920) Chaves, 1930 was redescribed by Kharchenko et al. (2004). It was considered by Lichtenfels et al. (1998) to be a species inquirenda.

Until recently *C. gyalocephaloides* Ortlepp, 1938 was considered (Lichtenfels et al., 1998) to be a species inquirenda. It has been redescribed (Lichtenfels et al., 2005) and differentiated from *C. insigne*. Lichtenfels et al. (2005) speculated that the large species of *Cylicocyclus* commonly found in zebras and donkeys in Africa, including *C. gyalocephaloides*, *C. adersi*, *C elongatus elongatus* and *C. auriculatus* may have originated in Africa in these hosts and given rise to the similar species *C. insigne* and *C. elongatus kotlani* parasitic in *E. caballus*.

6.8. *Poteriostomum Quiel, 1919*

Synonyms. *Hexodontostomum* Ihle, 1920.

General. Medium-sized Cyathostominea. MC inflated, high, ring-shaped, undivided. Posterior edge of MC at anterior edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae cone-shaped, short. Stalk of submedian papillae broader than long. Elements of ELC slightly more numerous and shorter than ILC elements. Elements of ELC longer than broad, tips pointed; insertion point on tips of ILC. Elements of ILC longer than broad, tips pointed; insertion point at anterior edge of BC. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, elongate, curving, thin at one end. Septum intracoronare origin on support. Medial

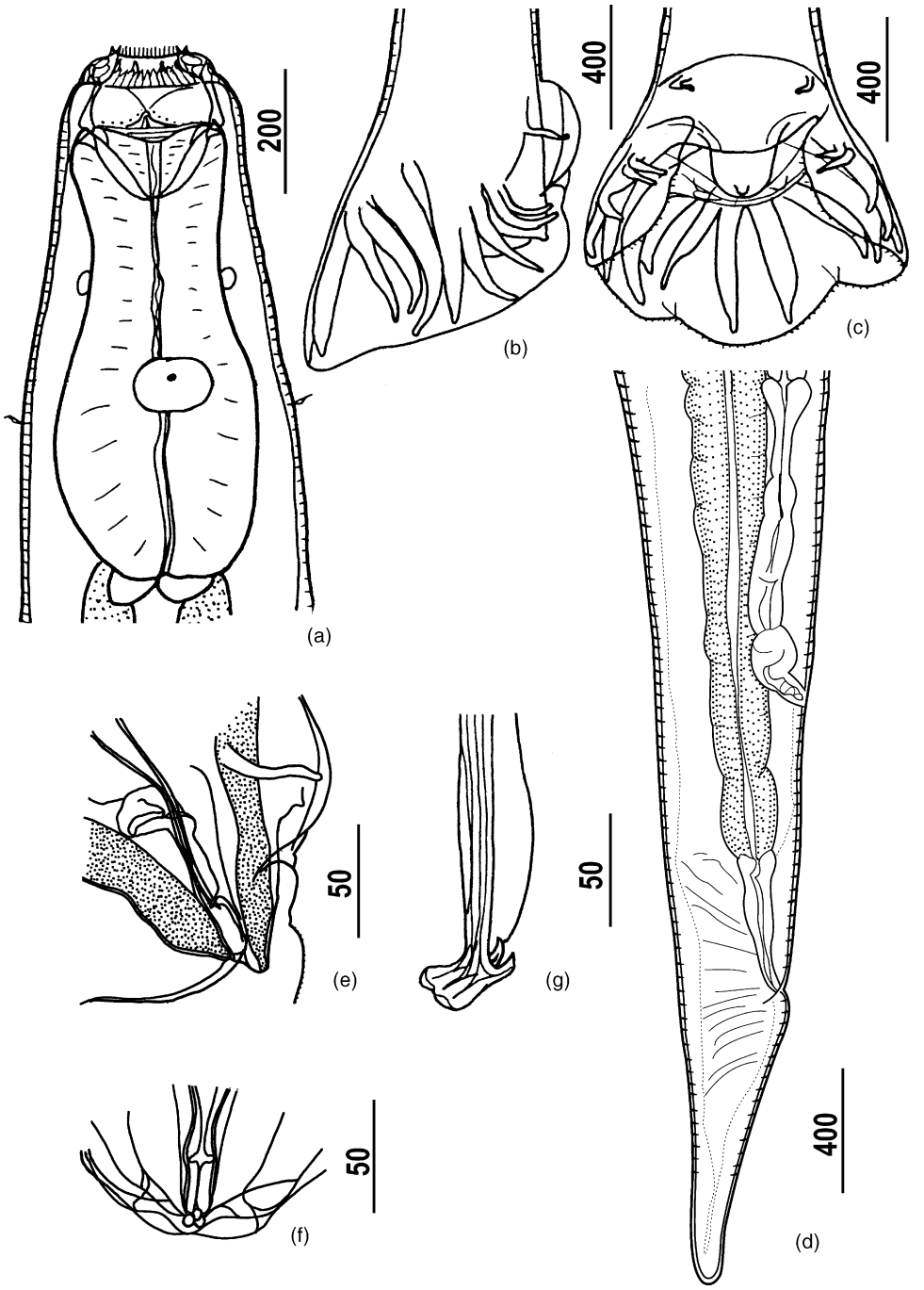

Fig. 103. *Poteriostomum imparidentatum.* (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (from Dvojnos and Kharchenko, 1994).

insertion of septum intracoronare situated at junction of ELC and ILC. Walls of BC straight, thicker posteriorly, but without ring-like thickening. Buccal cavity wider than deep, cylindrical. Dorsal gutter prominent, broad, less than $^1/_2$ of BC depth. Buccal teeth absent. Esophageal funnel moderately enlarged, lined with thick cuticle. Esophageal teeth not prominent. Anterior muscular portion of esophagus about $^1/_4$–$^1/_3$ of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

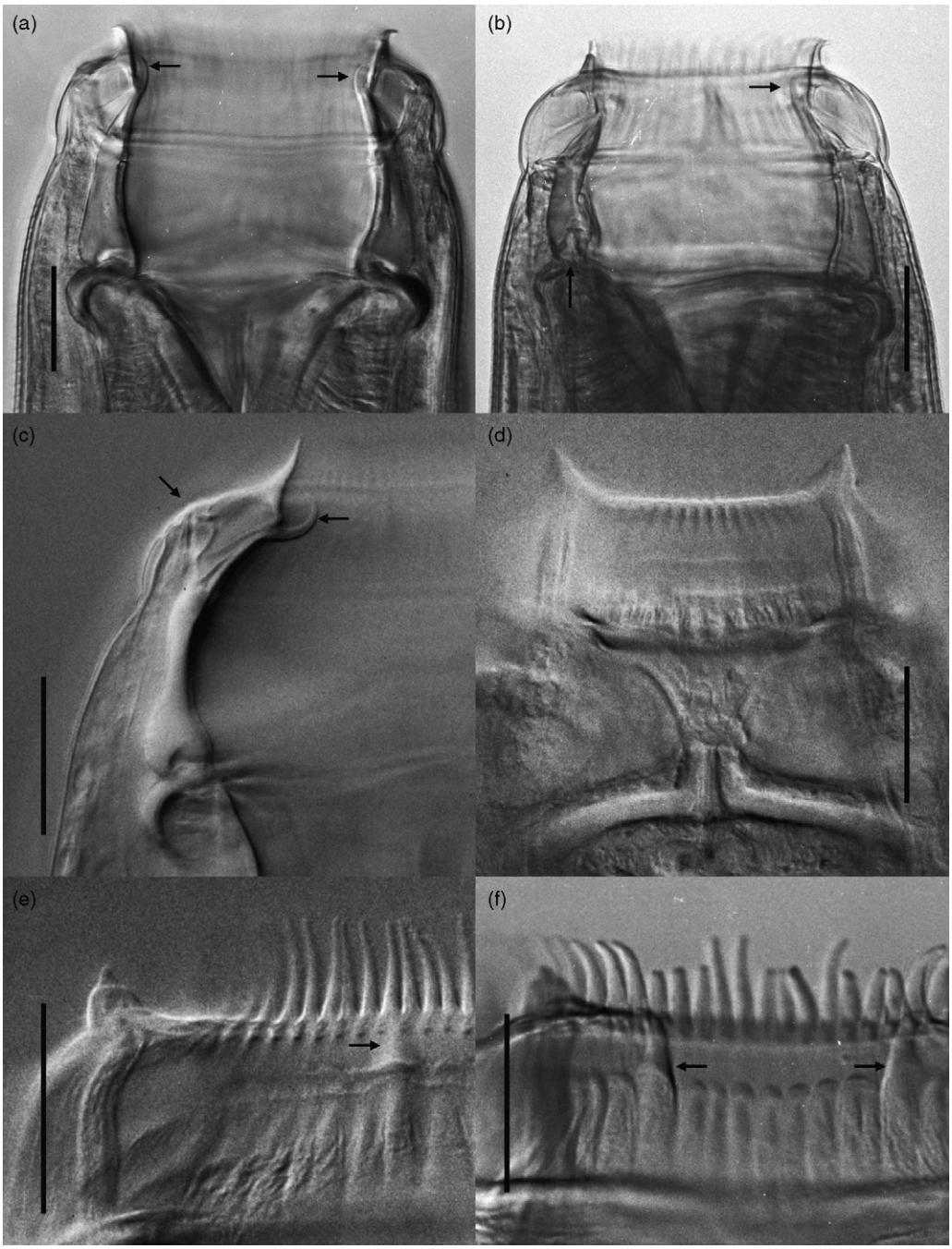

Fig. 104. *Poteriostomum imparidentatum.* (a) Buccal capsule, dorsoventral view. Arrows mark longer ILC elements. (b) Anterior end, lateral view, showing short dorsal gutter in BC wall at left. Arrow marks longer ILC element. (c) Anterior end, dorsal view, showing BC wall, lateral papilla (left arrow) and longer ILC element (right arrow). (d) Submedian papillae and dorsal gutter. (e) Submedian papilla. Arrow marks longer ILC element. (f) Elements of ELC (some with missing tips) and ILC. Arrows mark longer ILC elements (a, d, f modified from Lichtenfels, 1975).

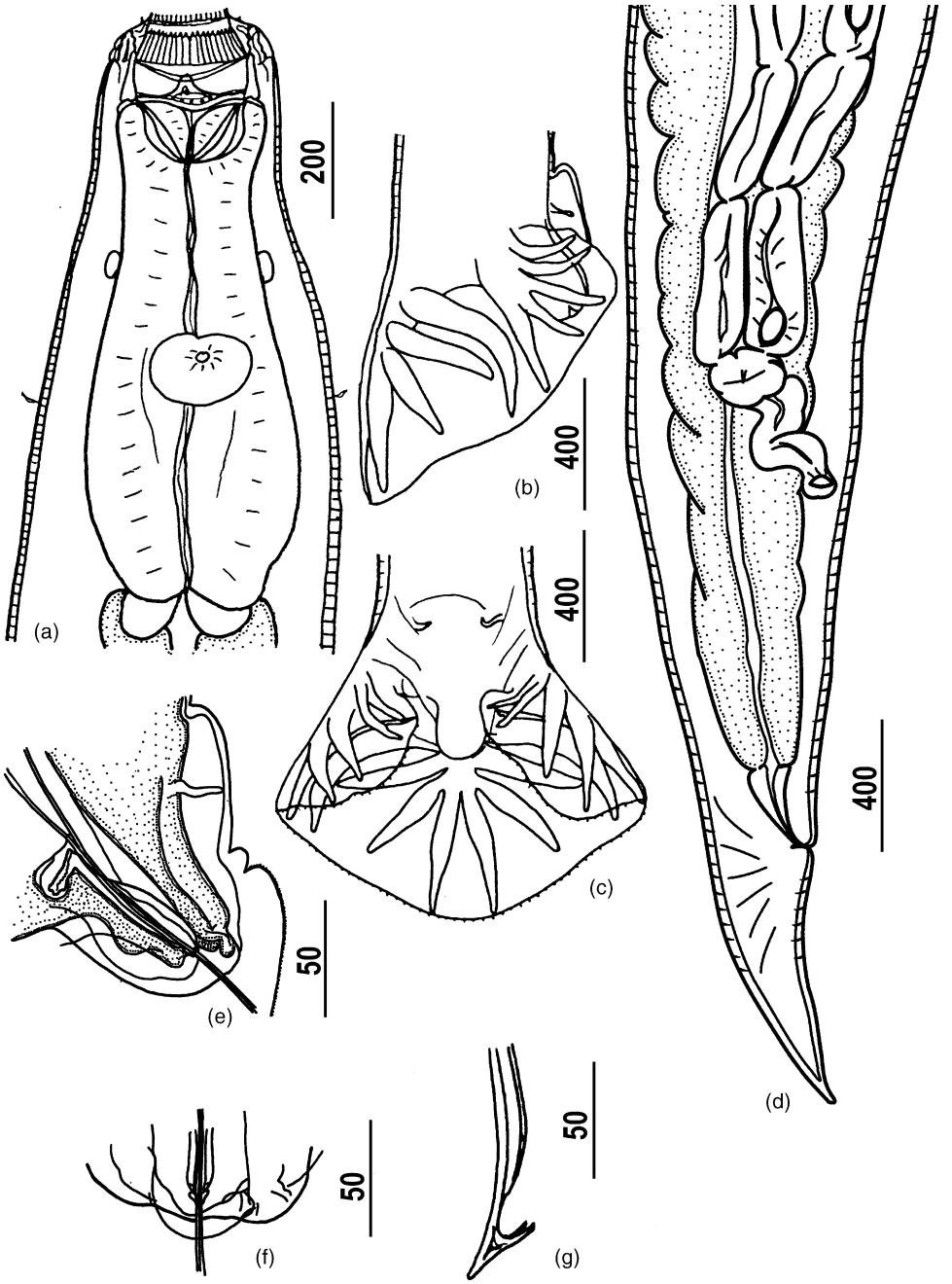

Fig. 105. *Poteriostomum ratzii*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

Male. Dorsal ray with six branches; origins of proximal and middle rays close together. Ventral rays shorter than laterals. Dorsal lobe longer then lateral lobes. Externodorsal rays origin on stem of dorsal. Gubernaculum large, with dorsal handle and ventral notch. Genital cone short, conical. Spicule tips hook- or harpoon-shaped.

Female. Vulva more than one tail length from anus. Vagina shorter than sphincter of ovejector. Ovejector vestibule oval or Y-shaped, infundibulum shorter than

sphincter. Tail conical, long, more than 2× diameter at anus.

Type species. *P. imparidentatum* Quiel, 1919.

6.8.1. Key to species of Poteriostomum

(1) a. Six elements of internal leaf-crown markedly longer than others. Spicule length less then 1.4 mm	*P. imparidentatum*
b. All elements of internal leaf-crown of equal lengths. Spicule length more then 1.4 mm	*P. ratzii*

6.8.2. *P. imparidentatum* Quiel, 1919 (Figs. 103 and 104)

Synonyms. *Cylicostomum imparidentatum* (Quiel, 1919) Ihle, 1920; *Cylichnostomum imparidentatum* (Quiel, 1919) Vevers, 1920; *Poteriostomum pluridentatum* Quiel, 1919; *Cylicostomum zebrae* Turner, 1920; Hexodontostomum markusi Ihle, 1920.

General. With characteristics of the genus. Elements of ELC shorter and more numerous(74–95) than ILC (38–59). Six elements ILC (two lateral and four submedial) longer than others. Excretory pore and deirids 460–550 from anterior end.

Male. Body length 11.5–14.0 mm. Esophagus length 611–706. BC width 183–256, depth 52–64. Spicule length 0.98–1.11 mm. Gubernaculum length 232–345. Dorsal ray length 370–620. Dermal collar well-developed on both sides of genital cone. Appendages of genital cone undeveloped. Protrusions of dermal collar absent.

Female. Body length 11.5–18.4 mm. Esophagus length 700–750. BC width 215–240, depth 66–70. Vulva to tail tip 1.60–1.79 mm. Anus to tail tip 0.65–1.0 mm. Egg size 96–108 × 48–56.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.8.3. *P. ratzii* (Kotlán, 1919) Ihle, 1920 (Figs. 105 and 106)

Synonyms. *Cylicostomum ratzii* Kotlán, 1919; *Cylichnostomum ratzii* (Kotlán, 1919) Yorke and Macfie, 1920; *Craterostomum ratzii* (Kotlán, 1919) Ostertag, 1932; *Poteriostomum ratzii nanum* Theiler, 1924.

General. With characteristics of the genus. Elements of ELC markedly shorter and more numerous than ILC (60–70 against 38–44). All elements of ILC equal length. Excretory pore and deirids 500–600 from anterior end.

Male. Body length 10.5–13.5 mm. Esophagus length 700–793. BC width 158–194, depth 49–64. Spicule length 1.5–1.76 mm. Gubernaculum length 232–286. Dorsal ray length 430–690. Dermal collar well-developed on both sides of genital cone. Appendages of genital cone undeveloped. Protrusions of dermal collar absent.

Female. Body length 14.5–20.0 mm. Length of esophagus 714–816. BC width 183–248, depth 51–73. Vulva to tail tip 1.5 –2.1 mm. Anus to tail tip 0.64–1.05 mm. Eggs size 95–115 × 50–57.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.8.4. Discussion

This genus is closely related to the genus *Parapoteriostomum*, especially in characteristics of the leaf-crown, size, and degree of splitting of the dorsal ray. The two genera can be separated easily, however, by characters of the buccal capsule, especially the point of insertion of the internal leaf-crown and the character of the dorsal ray. The species *P. imparidentatum* and *P. ratzii* are very similar except for the difference in the internal leaf-crown. Kotlán (1921) considered *P. imparidentatum* to be a variety of *P. ratzii*. However, they are recognized almost universally as distinct species.

According to Hartwich (1986) the females described by Galofré and Rosa (1944) as *P. imparidentatum var. longum* most likely belong to *P. ratzii* because no difference in size of the elements of the corona radiata interna are mentioned nor pictured; the smaller number of the elements of both leaf crowns corresponds more to that of *P. ratzii*. and the BC wall is significantly thicker than in *P. imparidentatum*.

Poteriostomum skrjabini Ershov, 1939 from the horse and ass in Russia, which was distinguished by a poorly defined dorsal gutter and a short tail with the vulva very close to the anus, is considered to be a *species inquirenda* following Lichtenfels et al. (1998).

6.9. Parapoteriostomum Hartwich, 1986

General. Medium-sized to large Cyathostominea. MC large and arched, undivided. Posterior edge of MC anterior or posterior to edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae bullet-shaped or round, short. Stalk

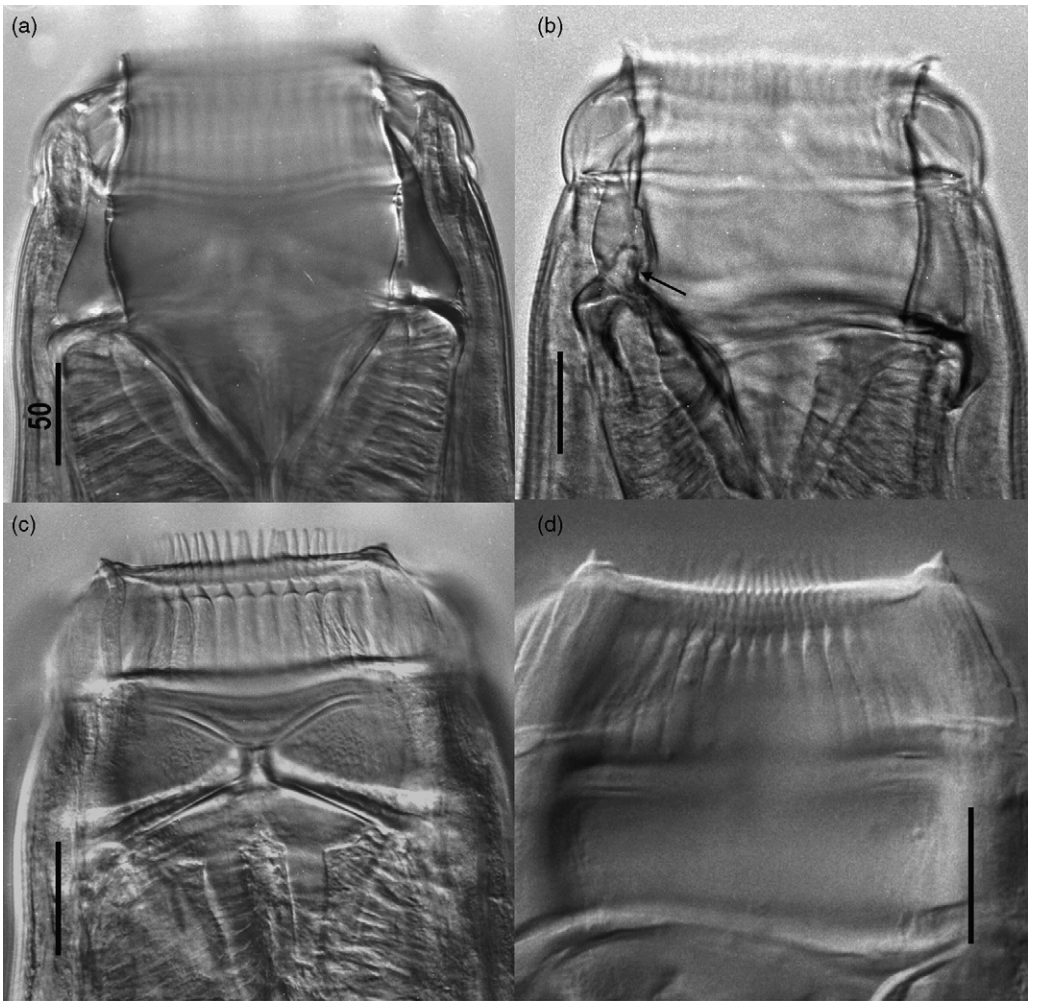

Fig. 106. *Poteriostomum ratzii*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, dorsal view, showing dorsal gutter in BC wall at left. (c) Anterior end, dorsal view, showing submedian papilla, long, broad ILC elements with triangular pointed tips, slender elements of ELC and short dorsal gutter. (d) Anterior end, lateral view, showing submedian papillae and elements of ILC and ELC (a–c modified from Lichtenfels, 1975).

of submedian papillae broader than long or longer than broad. Elements of ELC markedly more numerous and shorter than elements of ILC. Elements of ELC longer than broad, tips pointed; insertion point on tips of ILC. Elements of ILC longer than broad, tips pointed; insertion point at 1/4 or more of BC depth. Line formed by insertion of elements of ILC deeper in BC dorsally and ventrally than laterally. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, elongate, curving, thin at one end. Septum intracoronare origin on support (See Hartwich, 1986, Figs. 23 and 24, p. 81). Medial insertion of septum intracoronare situated at junction of ELC and ILC. Walls of BC straight in lateral view, or slightly convex in dorsoventral view, thicker anteriorly or posteriorly, with distinct notch at posterior edge. Buccal cavity wider than deep, wider posteriorly. Dorsal gutter button-like or absent. Buccal teeth absent. Esophageal funnel enlarged. Esophageal teeth not prominent. Anterior muscular portion of esophagus about 1/4–1/3 of esophagus length. Excretory pore posterior to NR. Deirids near EI.

Male. Dorsal ray with six branches. Ventral rays longer than laterals. Dorsal lobe longer then lateral lobes. Externodorsal rays origin on stem of dorsal ray or at junction of dorsal and laterals. Gubernaculum simple, without manubrium, and groove-like with paired ventral prominences. Genital cone sometime conspicuously long, extends beyond bursal edge. Spicule tips hook- or harpoon-shaped.

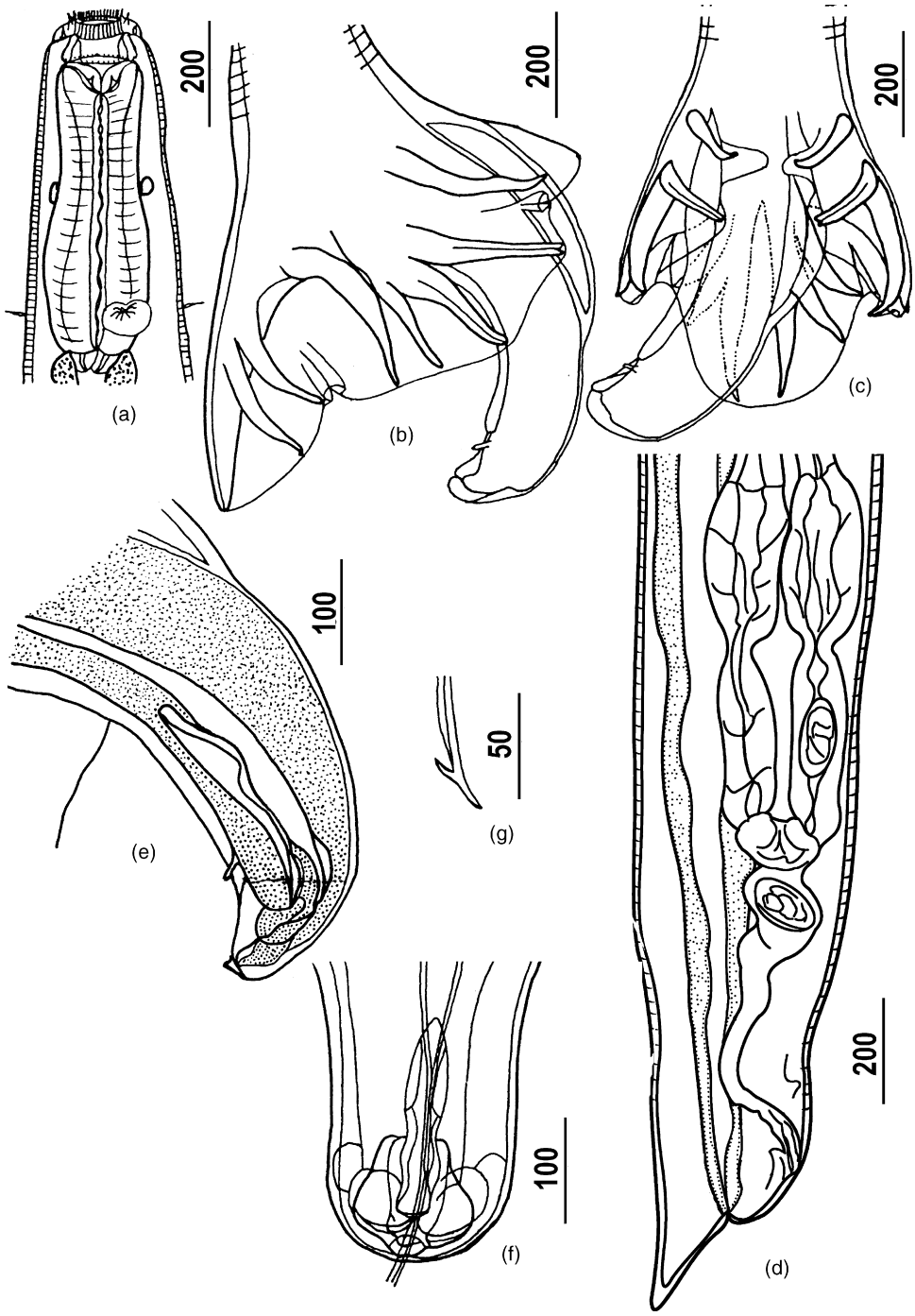

Fig. 107. *Parapoteriostomum mettami*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

Female. Vulva about one, or less than one tail length from anus. Vagina only slightly longer than sphincter of ovejector. Ovejector vestibule oval or Y-shaped, infundibulum slightly shorter than sphincter. Tail conical or digitiform, short, less than 2× diameter at anus.

Type species. *P. mettami* (Leiper, 1913) Hartwich, 1986.

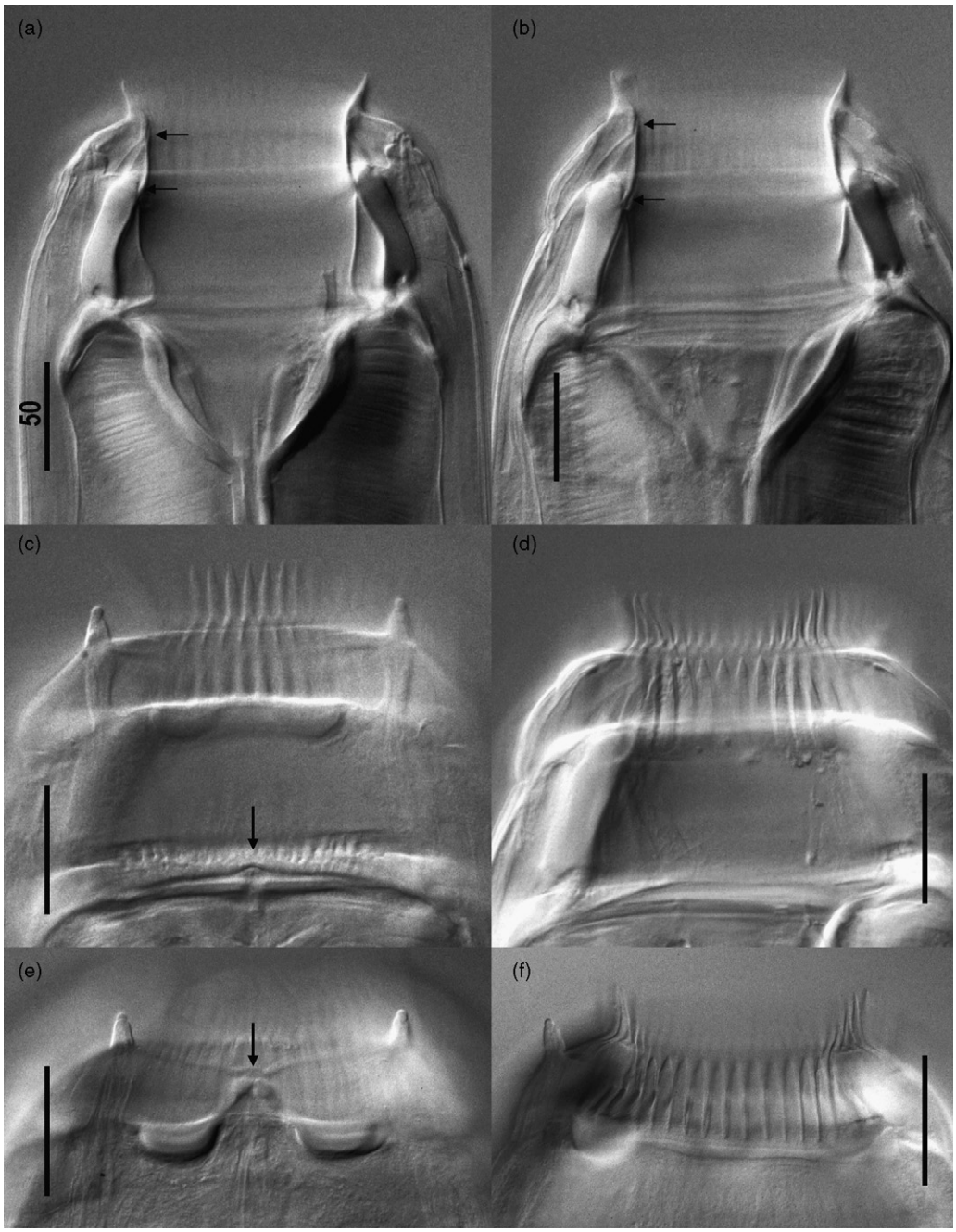

Fig. 108. *Parapoteriostomum mettami*. (a) Buccal capsule, dorsoventral view. Arrows mark anterior and posterior ends of ILC. (b) Buccal capsule, lateral view. Arrows mark anterior and posterior ends of ILC. (c) Elements of ELC, submedian papillae and dorsal gutter (arrow). (d) Elements of ILC and ELC. (e) Submedian papillae, lateral papilla (arrow) and parts of support flanking it. (f) Elements of ILC and ELC and one submedian papilla, sublateral view.

6.9.1. Key to species of Parapoteriostomum

(1) a. Elements of ILC less than twice as long as elements of ELC; ILC inserted at similar level on BC wall laterally, dorsally and ventrally — *P. mettami*

b. Elements of ILC more than twice as long as elements of ELC; ILC inserted on BC wall significantly more deeply ventrally and dorsally than laterally — 2

(2) a. BC walls thicker anteriorly, more that four times as long as greatest thickness — *P. euproctus*

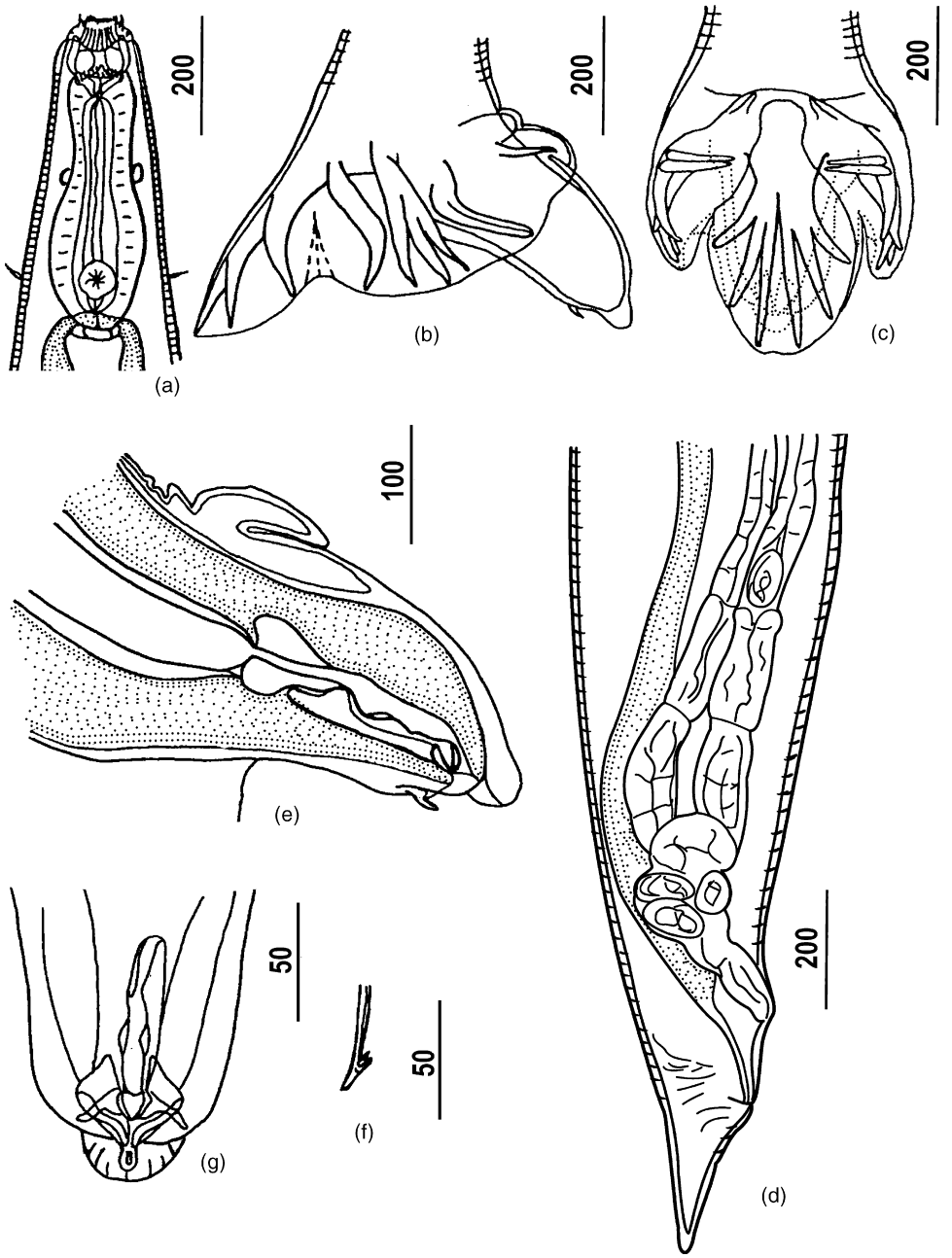

Fig. 109. *Parapoteriostomum euproctus*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

b. BC walls of uniform thickness or thicker posteriorly, length less than three times greatest thickness	3	
(3) a. BC walls of nearly uniform thickness; short dorsal gutter present; dorsal lobe of copulatory bursa more than twice as long as lateral bursal lobes		*P. schuermanni*
b. BC walls thickest posteriorly; dorsal gutter absent; dorsal lobe of copulatory bursa less than twice length of lateral bursal lobes		*P. mongolica*

6.9.2. P. mettami (Leiper, 1913) Hartwich, 1986 (Figs. 107 and 108)

Synonyms. *Cylicostoma mettami* Leiper, 1913; *Cylicostomum mettami* (Leiper, 1913) Ransom and Hadween, 1918; *Trichonema mettami* (Leiper, 1913) Le Roux, 1924; *Cylicocercus mettami* (Leiper, 1913) Cram, 1924; *Cylicostomum ihlei* Kotlán, 1921; *Cylicodontophorus mettami* (Leiper, 1913)

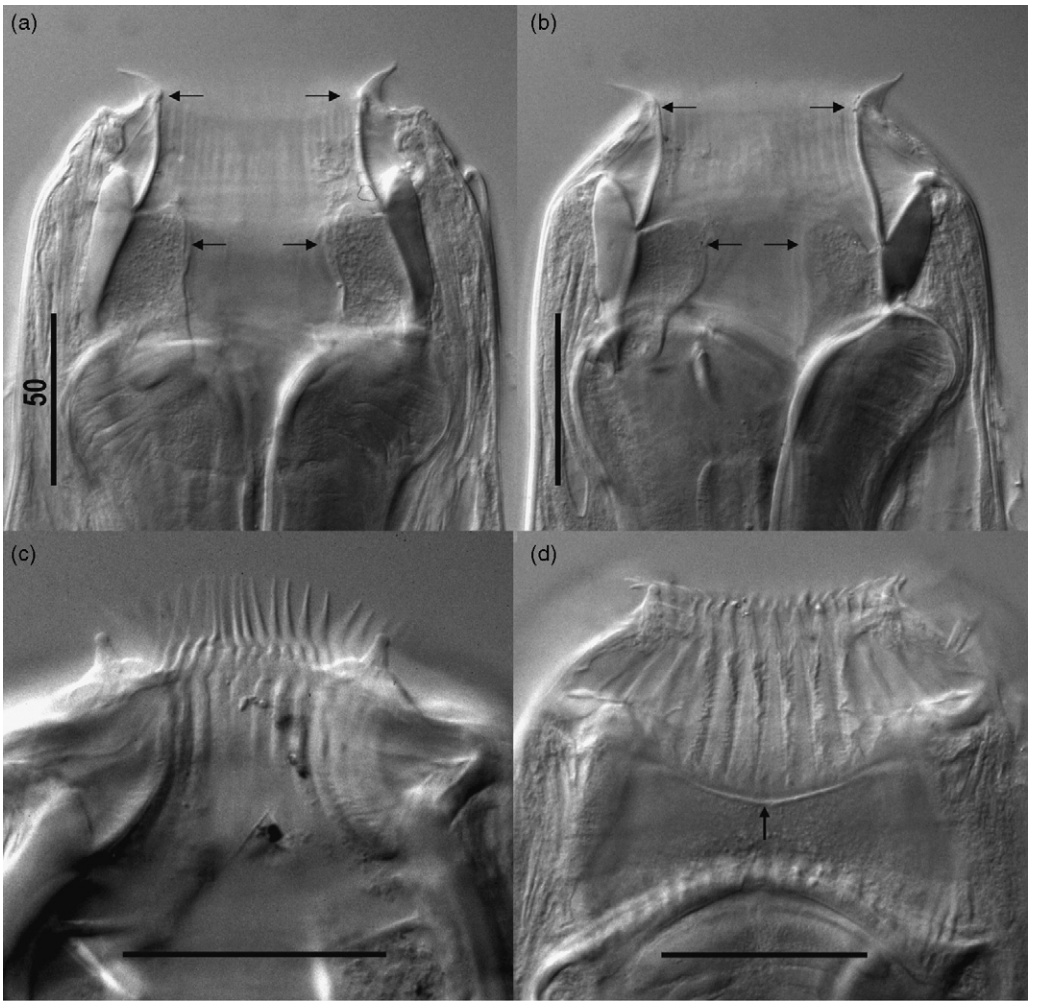

Fig. 110. *Parapoteriostomum euproctus*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view, showing junction of ILC and ELC (upper arrows) and inflated cuticular lining of BC (lower arrows). Arrow marks curved insertion line of ILC which is deeper dorsally and ventrally than laterally. (c) Elements of ELC and ILC. (d) Submedian papillae and elements of ILC and ELC, dorsal view. Arrow marks dorsal esophageal tooth.

Foster, 1936; *Cylicodontophorus zhongweiensis* Li and Li, 1993.

General. Large-sized Cyathostominea. Posterior edge of MC posterior to anterior edge of BC. ELC elements markedly more numerous (60) than ILC elements (40–46). ILC elements less than twice as long as ELC elements. Insertion point for posterior ends of elements of ILC about 1/4 of BC depth dorsally and ventrally; slightly less laterally. Dorsal gutter button-like. Esophageal funnel well-developed.

Male. Body length 9.9–10.6 mm. Esophagus length 545–574. BC width 98–117, depth 46–59. Distance from deirids and excretory pore to head end 502–574. Spicule length 1.95–2.3 mm. Gubernaculum length 234–258. Dorsal ray length 443–473. Dermal collar undeveloped. Appendages of genital cone paired small finger-shaped projections. Protrusions of dermal collar absent.

Female. Body length 12.7–16.2 mm. Esophagus length 631–717. BC width 130–143, depth 46–59. Distance from deirids and excretory pore to head end 574–688. Vagina length 800. Vulva to tail tip 375–470. Anus to tail tip 250–300. Egg size 124–128 × 60–62.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.9.3. P. euproctus (Boulenger, 1917) Hartwich, 1986 (Figs. 109 and 110)

Synonyms. *Cylichnostomum euproctus* Boulenger, 1917; *Cylicostomum euproctus* (Boulenger, 1917)

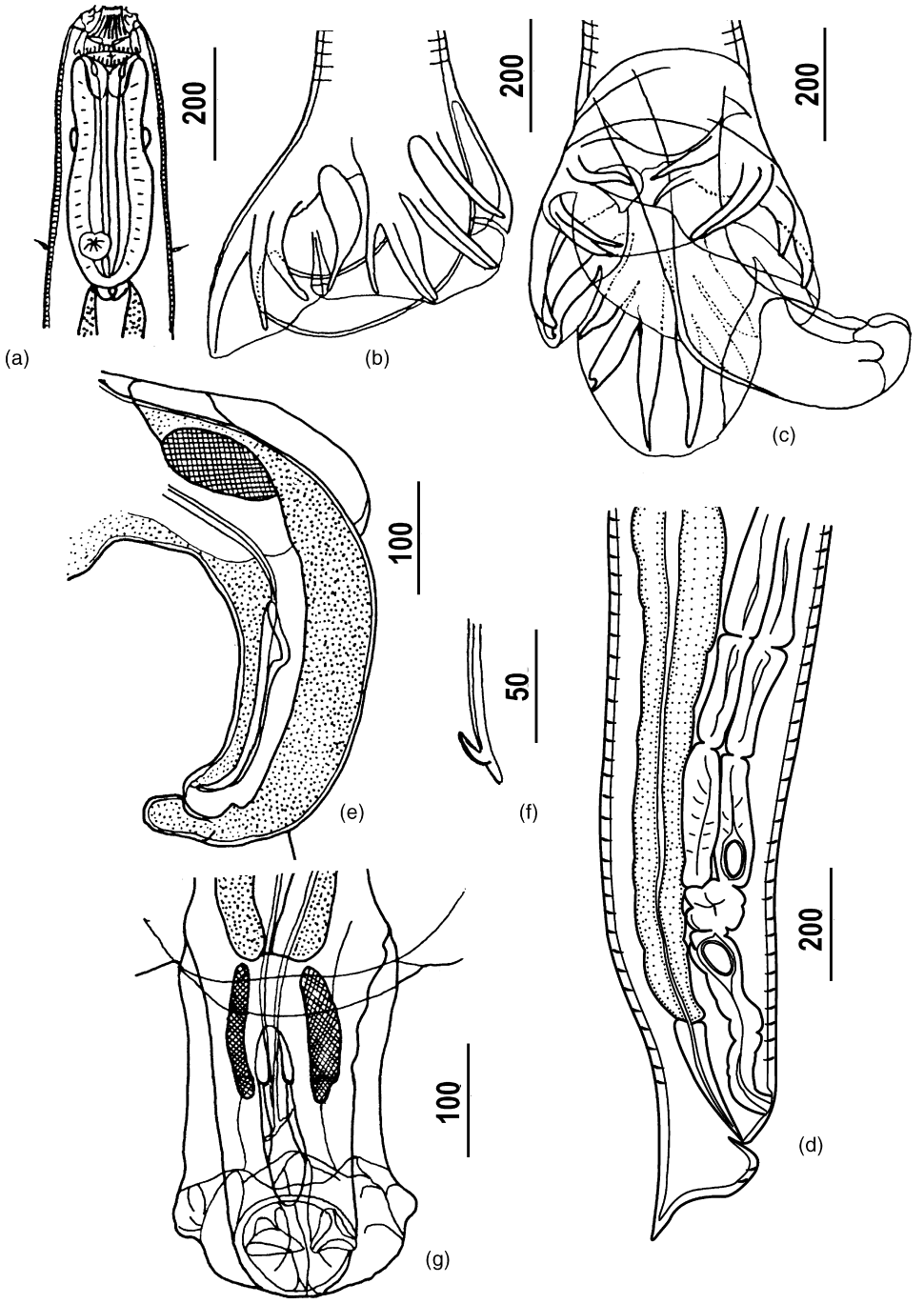

Fig. 111. *Parapoteriostomum mongolica*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

Ransom and Hadween, 1918; *Trichonema euproctus* (Boulenger, 1917) Le Roux, 1924; *Cylicodontophorus euproctus* (Boulenger, 1917) Cram, 1924.

General. Medium-sized Cyathostominea. Posterior edge of MC anterior to edge of BC. ELC elements more numerous (38–40) than elements of ILC (30–34). ILC more than twice as long as ELC. Insertion point for posterior ends of elements of ILC about 1/4 of BC depth laterally and 1/3−1/2 ventrally and dorsally. Dorsal gutter inconspicuous. Esophageal funnel shallow.

Male. Body length 6.75–7.3 mm. Esophagus length 360–420. BC width 75–100, depth 28–40. Distance

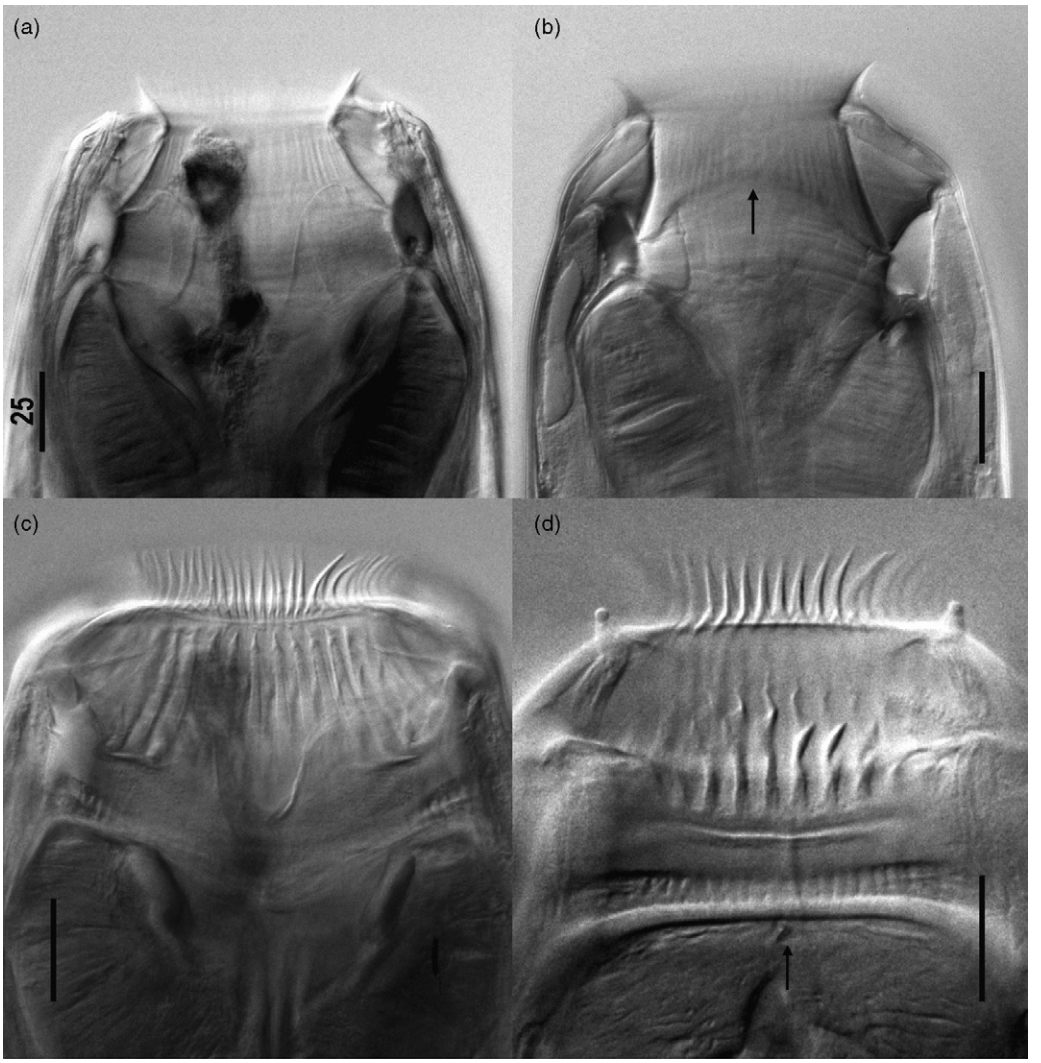

Fig. 112. *Parapoteriostomum mongolica*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. Arrow marks curved insertion line of ILC, which is deeper dorsally and ventrally than laterally (c) Elements of ELC and ILC. (d) Submedian papillae and elements of ILC and tiny dorsal gutter (arrow).

from deirids and excretory pore to head end 360–500. Spicule length 1.36–2.24 mm. Gubernaculum length 160–230. Dorsal ray length 300–320. Dermal collar poorly developed on proximal part of ventral side of genital cone. Appendages of genital cone paired, middle-sized, finger-shaped expanded proximally. Protrusions of dermal collar absent.

Female. Body length 6–9.5 mm. Esophagus length 360–410. BC width 72–105, depth 28–40. Vagina length 360–460. Vulva to tail tip 300–400. Anus to tail tip 190–250. Egg size 80–100 × 50–60. Tail of mature females straight, tip sharply pointed

Hosts. Equus caballus, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.9.4. P. mongolica (Tshoijo in Popova, 1958) Lichtenfels et al., 1998 (Figs. 111 and 112)

Synonyms. *Cylicodontophorus mongolica* Tshoijo in Popova (1958).

General. Medium-sized Cyathostominea. Posterior edge of MC situated at anterior edge of BC. ELC elements markedly more numerous (54–60) than elements of ILC (33–38). ILC more than twice as long as ELC. Insertion point of ILC at more than 1/2 depth of BC, ventrally and dorsally, but at 1/4 of BC depth laterally. Dorsal gutter button-like Esophageal

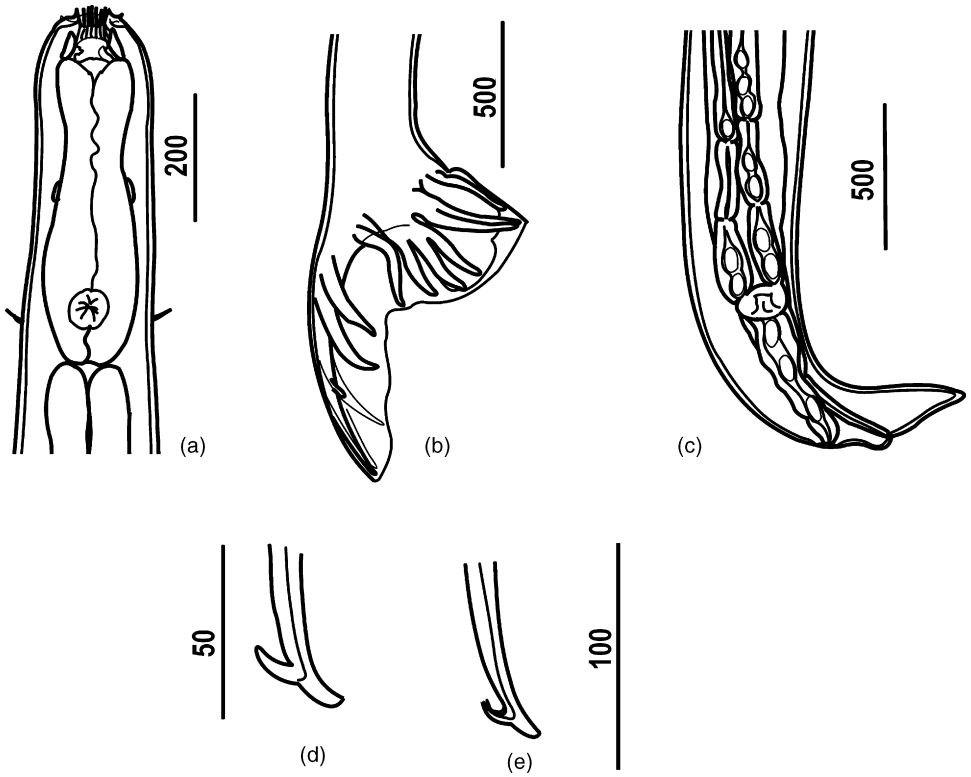

Fig. 113. *Parapoteriostomum schuermanni*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Tail of female. d, (e) Fused spicule tips of male.

funnel moderately developed, with thick cuticular lining.

Male. Body length 7.0–8.1 mm. Esophagus length 370–420. BC width 99–150, depth 39–44. Anterior end to: deirids 403–448; excretory pore 381–454. Spicule length 1.57–1.85 mm. Gubernaculum length 183–213. Dorsal ray length 336–392. Dermal collar poorly developed on proximal part of ventral side of genital cone. Appendages of genital cone and protrusions of dermal collar absent.

Female. Body length 8.3–11.6 mm. Esophagus length 437–504. BC width 99–150, depth 39–50 (21–33 according Tschoijo, 1957). Anterior end to: deirids 420–504; excretory pore 414–492. Vulva to tail tip 246–314. Anus to tail tip 162–241. Egg size 105–111 × 50–54.

Hosts. *Equus caballus*.

Locality. Cecum, colon.

Distribution. Asia.

6.9.5. *P. schuermanni* (Ortlepp, 1962) Hartwich, 1986 (Figs. 113 and 114)

Synonyms. *Trichonema* (*Cylicodontophorus*) *schuermanni* Ortlepp, 1962.

General. Medium-sized Cyathostominea. Posterior edge of MC situated at anterior edge of BC. ELC elements markedly more numerous (50) than elements of ILC (25). ILC more than twice as long as ELC. Insertion point for posterior ends of elements of ILC about 1/4 of BC depth laterally and 1/4−1/3 ventrally and dorsally. Dorsal gutter relatively well-developed, short and broad. Esophageal funnel shallow.

Male. Body length 6 mm. Esophagus length 470. BC width 130, depth 60. Anterior end to: deirids 570; excretory pore 870. Spicule length 1.8 mm. Gubernaculum length 250. Dorsal ray length 1.2 mm. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone slender flexible and flagella-like. Protrusions of dermal collar absent.

Female. Body length 9 mm. Esophagus length 600–630. BC width 133, depth 62. Vulva to tail tip 390–510. Anus to tail tip 240–330. Egg size 102 × 50.

Hosts. *E. burchelli*.

Locality. Cecum, colon.

Distribution. Africa.

6.9.6. Discussion

Hartwich (1986) erected *Parapoteriostomum* for three species formerly in the genus *Cylicodontophorus*,

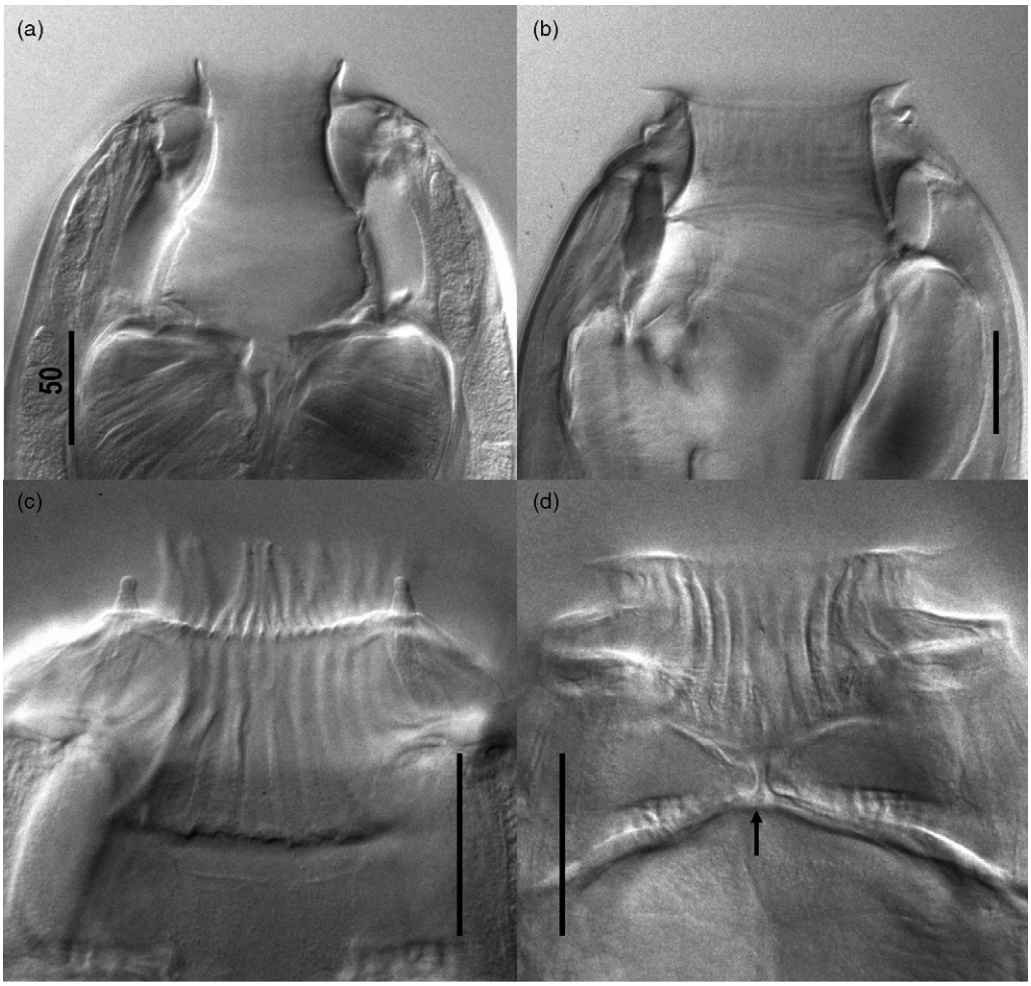

Fig. 114. *Parapoteriostomum schuermanni*. (a) Buccal capsule, dorsoventral view. (b) Buccal capsule, lateral view. (c) Elements of ELC and ILC and submedian papillae. (d) Dorsal gutter (arrow) and elements of ILC.

which shared with *Poteriostomum* these and other characteristics, a mouth collar not divided into two rings, septum intracoronare extending from the middle of the support to the junction of the leaf-crowns, elements of ELC fewer and shorter than ILC. Lichtenfels et al. (1998) added *P. mongolica* to this genus, a species described originally in the genus *Cylicodontophorus*, and redescribed by Dvojnos and Kharchenko (1988). Based on the English abstract of the description of *Cylicodontophorus zhongweiensis* Li and Li, 1993, this species was synonomized (Lichtenfels et al., 1998) with *P. mettami*. However, Zhang and K'ung (2002) continued to recognize *C. zhongweiensis* and placed it in *Parapoteriostomum*. Zhang and K'ung (2002) placed a species in *Parapoteriostomum* that we recognized as *Cylicodontophorus reineckei*.

The independence of *Parapoteriostomum* and its relationship to *Poteriostomum* recognized by Hartwich (1986) are strongly supported by the molecular data of Hung et al. (2000).

6.10. *Hsiungia K'ung and Yang, 1964*

General. Middle-sized Cyathostominea. MC inflated, high, ring-shaped, divided into inner and outer rings. Posterior edge of MC at anterior edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae bullet-shaped, twice as long as broad. Stalk of submedian papillae longer than broad. Number of elements of ELC equal, or nearly so, to ILC. ELC equal to ILC in length. Elements of ELC longer than broad, tips pointed; insertion point on tips of ILC. Elements of ILC longer than broad, tips pointed; insertion on anterior edge of BC. Line formed by insertion of elements of ILC straight. Form of

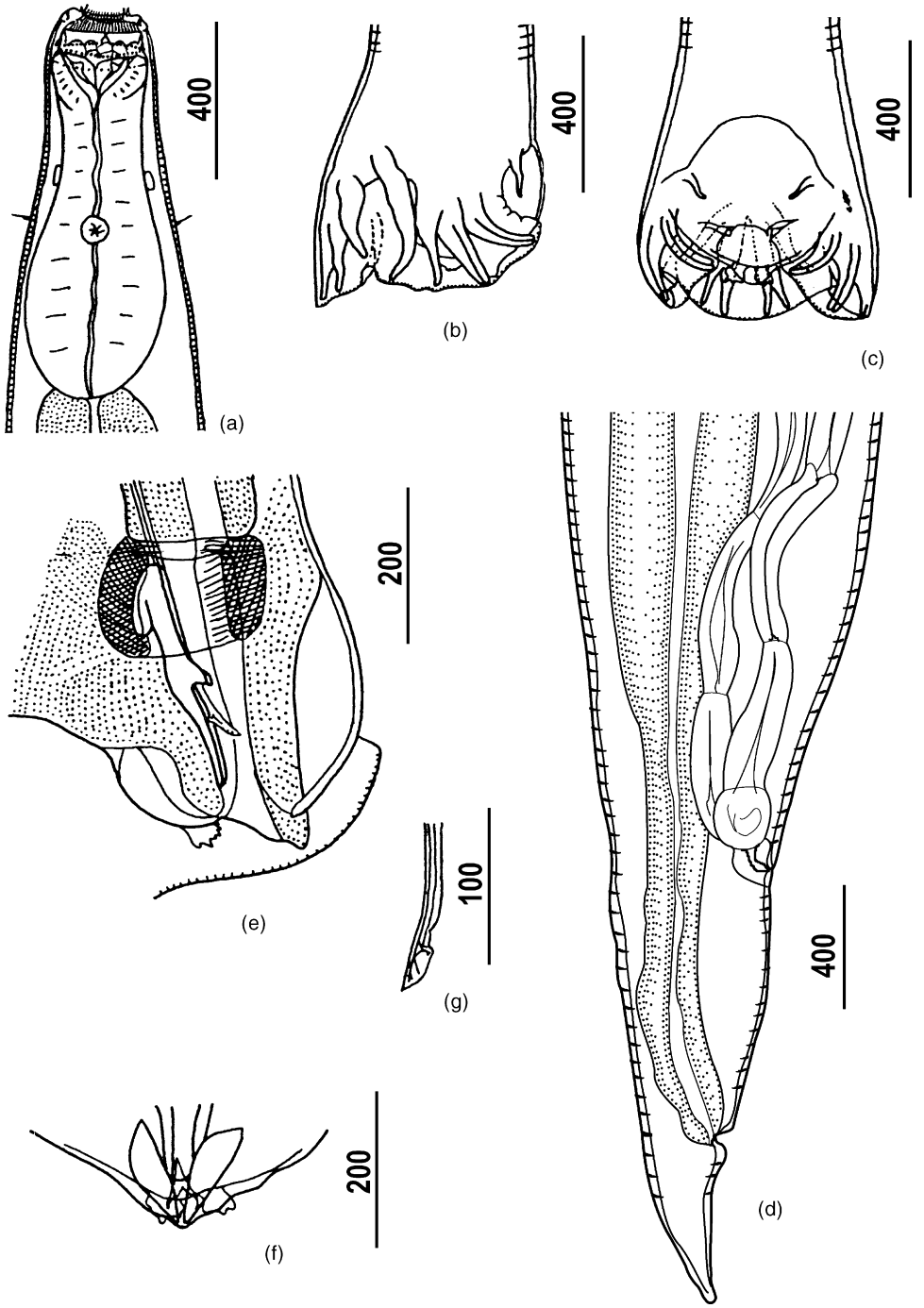

Fig. 115. *Hsiungia pekingensis*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, elongate, curving, thin at one end. Septum intracoronare origin on support. Medial insertion of septum intracoronare situated at junction of ELC and ILC. Walls of BC straight, thickening gradually to greatest thickness at base. Buccal cavity wider than deep, cylindrical. Dorsal gutter nipple- or button-like. Buccal teeth

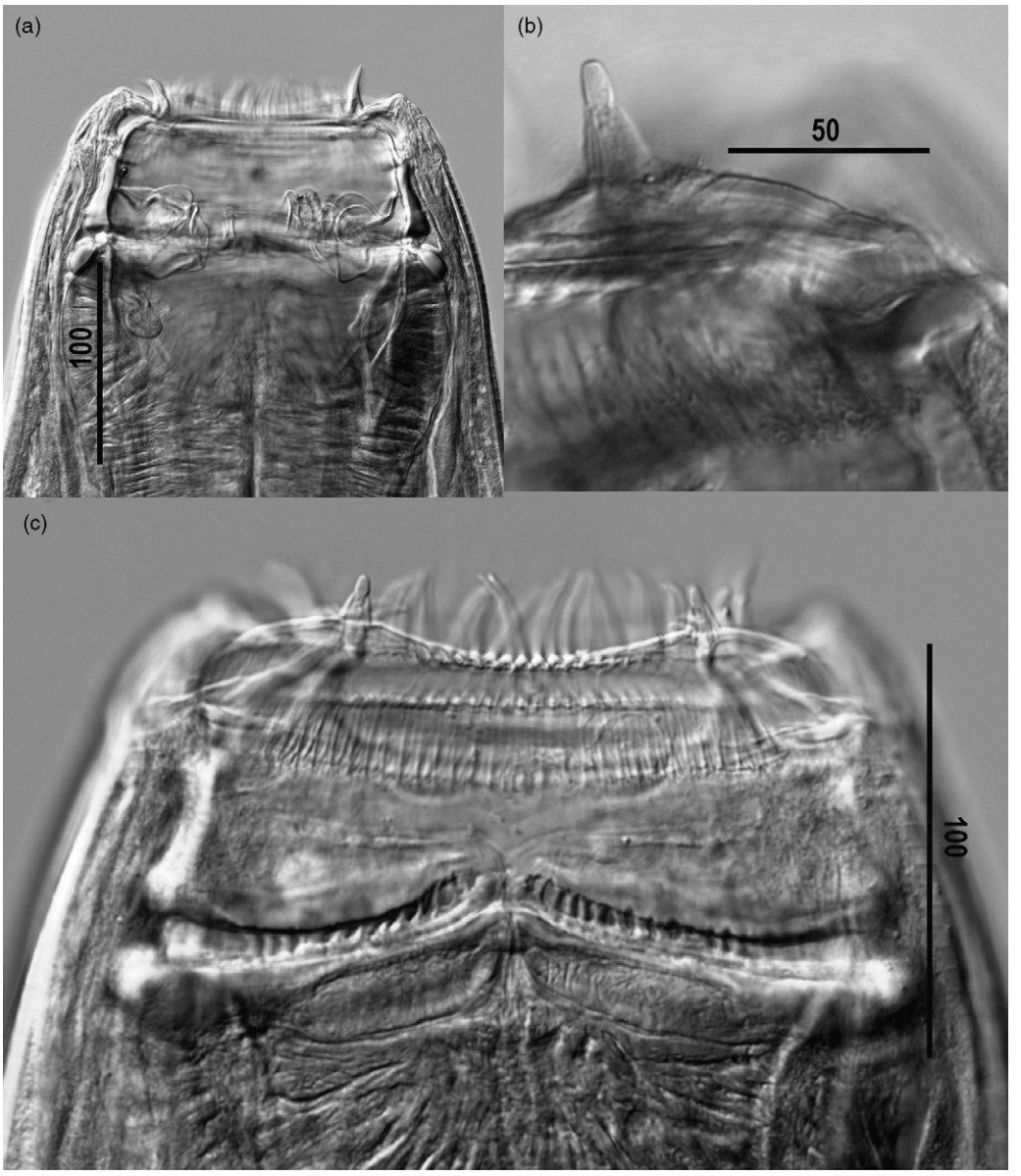

Fig. 116. *Hsiungia pekingensis*. (a) Buccal capsule, dorsoventral view. (b) Submedian papilla. (c) Buccal capsule, dorsal view, showing elements of ELC and ILC, submedian papillae and dorsal gutter.

absent. Esophageal funnel enlarged. Esophageal teeth prominent. Anterior muscular portion of esophagus about $^{1}/_{4}-^{1}/_{3}$ of esophagus length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches. Ventral rays longer than laterals. Dorsal lobe equal in length to lateral lobes. Externodorsal rays origin at junction of dorsal and laterals. Gubernaculum large, with dorsal handle and ventral notch. Genital cone short, conical. Spicule tips straight or slightly curved.

Female. Vulva two to three, or more, tail lengths from anus. Vagina shorter than sphincter of ovejector. Ovejector vestibule oval or Y-shaped, infundibulum about equal to sphincter. Tail conical, long, more than 2× diameter at anus.

Type species. *H. pekingensis* K'ung and Yang, 1964.

6.10.1. H. pekingensis K'ung and Yang, 1964 (Figs. 115 and 116)

Synonyms. Cylicocyclus (Hsiungia) pekingensis K'ung and Yang, 1964.

General. With characteristics of genus.

Male. Body length 9.0–12.3 mm (15.8–17.0 mm according K'ung and Yang, 1964). Esophagus length 701–958. BC width 132–156, depth 39–51. Anterior end to: deirids 514–615; excretory pore 486–586; NR 400–457. Spicule length 1.18–1.3 mm. Gubernaculum length 237–270. Dorsal ray length (to base of externodorsal ray) 228–414. Dermal collar well-developed around genital cone. Appendages of genital cone paired, separate, oval, slightly flattened dorso-ventral projections.

Female. Body length 12.1–16.6 mm (18.5–20.5 mm according to K'ung and Yang, 1964). Esophagus length 801–958. BC width 177–207, depth 45–57. Anterior end to: deirids 601–744; excretory pore 586–744; NR 429–543. Vulva to tail tip 0.99–1.52 mm. Anus to tail tip 415–572. Egg size 114–150 × 54–72.

Hosts. *Equus caballus*, *E. asinus*.

Locality. Cecum, colon.

Distribution. Asia.

6.10.2. Discussion

This species, while similar to *Cylicocyclus* in shape of the wall of the buccal capsule, has some primitive characters not present in that genus, including a short anteriorly placed vagina and a spicule without an anchor shaped tip and with alae. The single species of *Hsiungia*, *H. pekingensis*, appears, to be closer to *Poteriostomum* than to *Cylicocyclus* except for the male bursa. This interesting species must be studied further to determine its relationship within the Cyathostominea. It is hoped that recognition at the genus level, following Dvojnos and Kharchenko (1988), will stimulate study of this species.

6.11. *Cylindropharynx* Leiper, 1911

General. Small to medium-sized Cyathostominae. MC flattened, divided into inner and outer rings. Posterior edge of MC posterior to edge of BC. Amphids not markedly projected through MC surface. Tip and longer stalk of submedian papillae extend through MC. Tip of submedian papillae spindle-shaped, two to four times as long as thick. Stalk of submedian papillae longer than broad. ELC consists of six triangular elements unequal in size, four submedian and equal, relatively small size; two leaves much broader and lateral, usually notched at apex and longitudinally grooved. External leaf crown deficient dorsally and ventrally, but from each prominent dorsal and ventral lips of mouth collar a broad crescentic plate projects medially. ELC insertion point on tips of ILC, but slightly back from tips. Twelve elements of ILC longer than broad, tips pointed; insertion less than 1/4 of BC depth. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC adorned with hooks or projections. Support for ELC surrounds anterior edge of BC, helmut-like. Septum intracoronare origin on support. Medial insertion of septum intracoronare situated at junction of ELC and ILC. Walls of BC concave, thicker in middle. Buccal cavity much deeper than wide, oval or cylindrical. Dorsal gutter nipple- or button-like. Buccal teeth absent. Esophageal funnel moderately enlarged. Esophageal teeth prominent. Anterior muscular portion of esophagus less than 1/4 of length. Excretory pore posterior to NR. Deirids near middle of glandular esophagus.

Male. Proximal and middle branches of dorsal rays fused. Ventral rays shorter than laterals. Dorsal lobe equal in length to laterals. Externodorsal rays origin at junction of dorsal and laterals. Gubernaculum with small handle, enlarged distal tip. Genital cone elongate, extends beyond bursal edge. Spicule tips hook- or harpoon-shaped.

Female. Vulva two to three, or more, tail lengths from anus. Vagina shorter than sphincter of ovejector. Ovejector vestibule T-shaped, infundibulum longer than sphincter. Tail conical, short, less than twice diameter at anus.

Type species. *C. brevicauda* Leiper, 1911.

Species inquirenda. *C. rhodesiensis* Yorke and Macfie, 1920

6.11.1. Key to species of *Cylindropharynx*

(1) a. BC depth less than 240 μm. Buccal cavity elongate oval. Tip of external branch of dorsal ray undivided. Female tail long 1.1–1.7 mm	*C. longicauda*
b. BC depth more than 270 μm. Buccal cavity width greatest in first 1/3 of its depth and narrowed at middle. Tip of external branch of dorsal ray divided	2
(2) a. Female tail short. Distance from vulva to tail tip less than 1 mm	*C. brevicauda*
b. Female tail long. Distance from vulva to tail tip more than 1 mm	*C. intermedia*

6.11.2. *C. brevicauda* Leiper, 1911 (Figs. 117 and 118)

Synonyms. *C. aethiopica* Roetti, 1947.

General. Buccal cavity widest at first 1/3 of its depth and narrowed at middle.

Male. Body length 5.0–8.3 mm. Esophagus length 470–530. BC width 90–116, depth 280–400. Anterior end to: deirids 393–450; excretory pore 368–405; NR

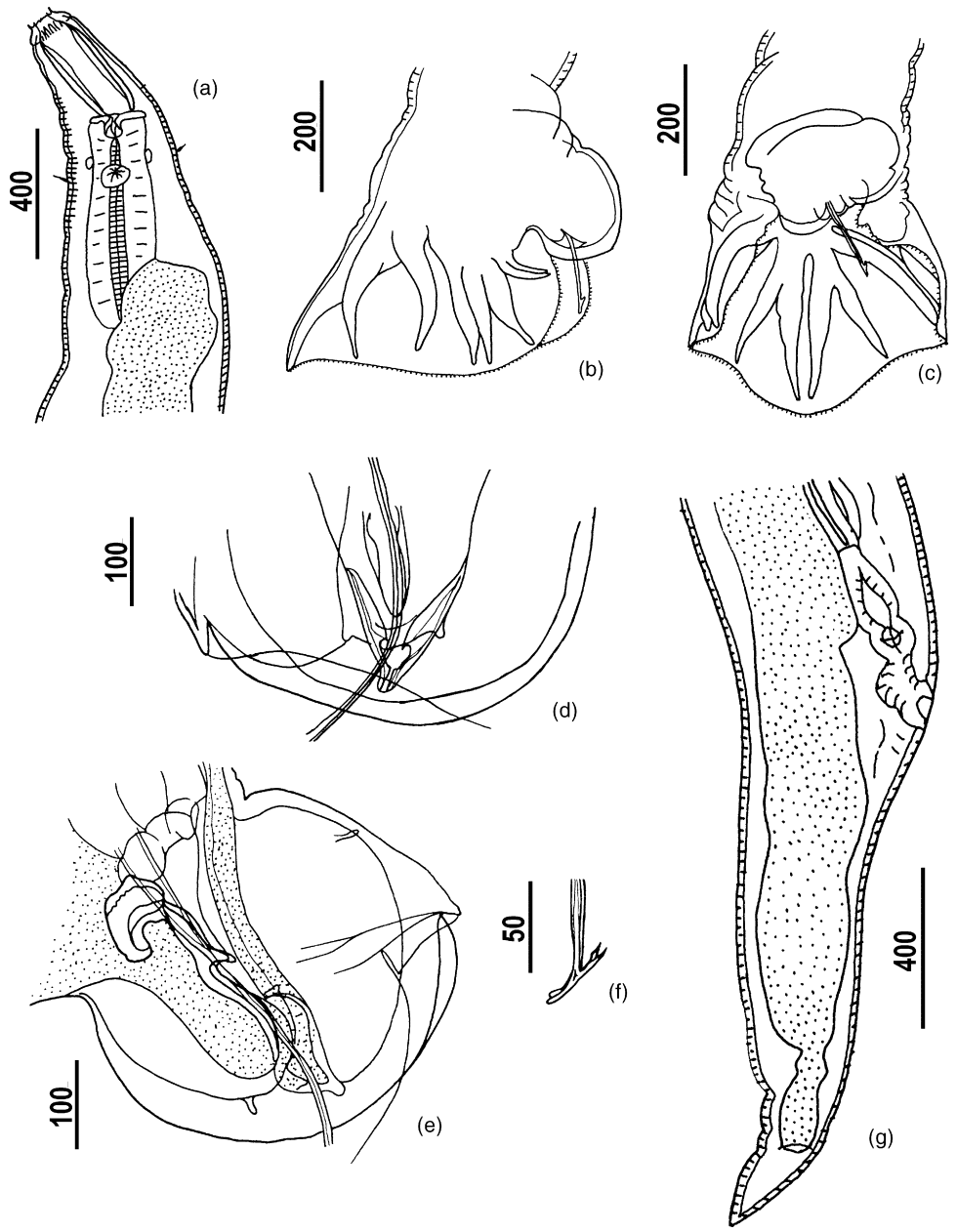

Fig. 117. *Cylindropharynx brevicauda*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tip of genital cone, ventral view. (d) Genital cone, lateral view. (f) Fused spicule tips of male. (g) Tail of female (modified from Dvojnos and Kharchenko, 1994).

319–325. Copulatory bursa delicately denticulated. Spicule length 0.96–1.10 mm. Gubernaculum length 122–146. Dorsal ray length 207–220. Genital cone size variable. Dermal collar well-developed on ventral side of genital cone. Genital cone appendages paired, finger-shaped, with rounded ends and irregular number of delicate pointed processes scattered over dorsal surface. Protrusions of dermal collar absent.

Female. Body length 5.6–10.1 mm, esophagus length 460–530. BC width 100–120, depth 280–400. Anterior end to: deirids 393–450; excretory pore 417–450; NR 319–356. Vulva to tail tip 397–988. Anus to tail tip 85–189. Egg size 88–92 × 44–49.

Hosts. *E. asinus*, *E. caballus* × *E. asinus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Africa.

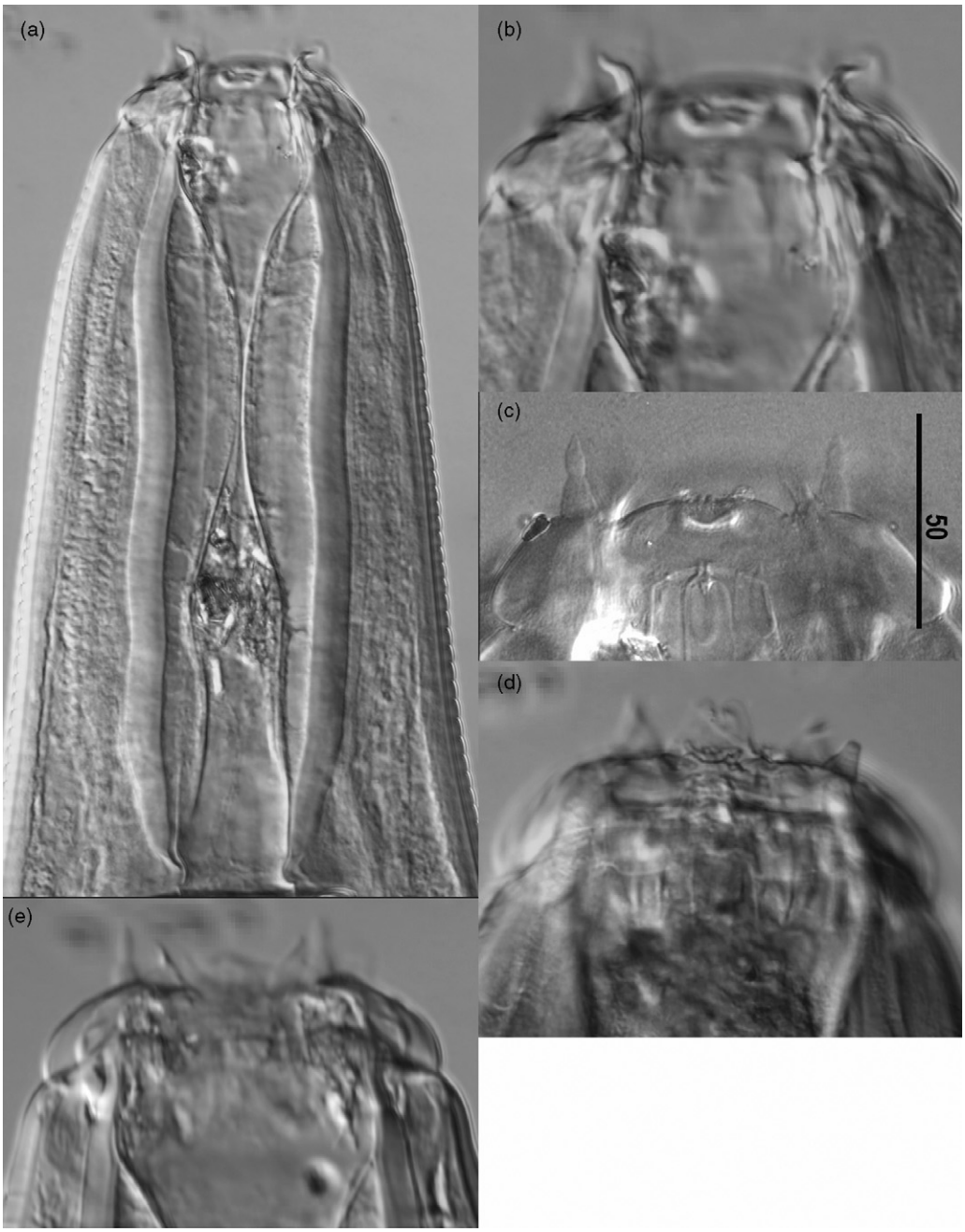

Fig. 118. *Cylindropharynx brevicauda*. (a) Buccal capsule, lateral view. (b) Elements of ELC and ILC, lateral view. (c) Submedian papillae, elements of ILC and ELC. (d) Submedian papillae, mouth collar and anterior edge of BC. (e) Structure of mouth collar and support for ELC.

6.11.3. C. intermedia Theiler, 1924 (Figs. 119 and 120)

Synonyms. *C. ornata* Cram, 1925, *C. dollfusi* Le Van Hoa, 1961.

General. Buccal cavity widest in first 1/3 of depth and narrowed at middle.

Male. Body length 7.6–10 mm. Esophagus length 470–603. BC width 85–120, depth 325–460. Anterior end to: deirids 475–672; excretory pore 510–672; NR 452–591. Spicule length 630–920. Gubernaculum length 200–260. Dorsal ray length 180–300. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone as in type species. Protrusions of dermal collar absent.

Female. Body length 8.4–11 mm. Esophagus length 580–747. BC width 100–166, depth 350–520. Anterior

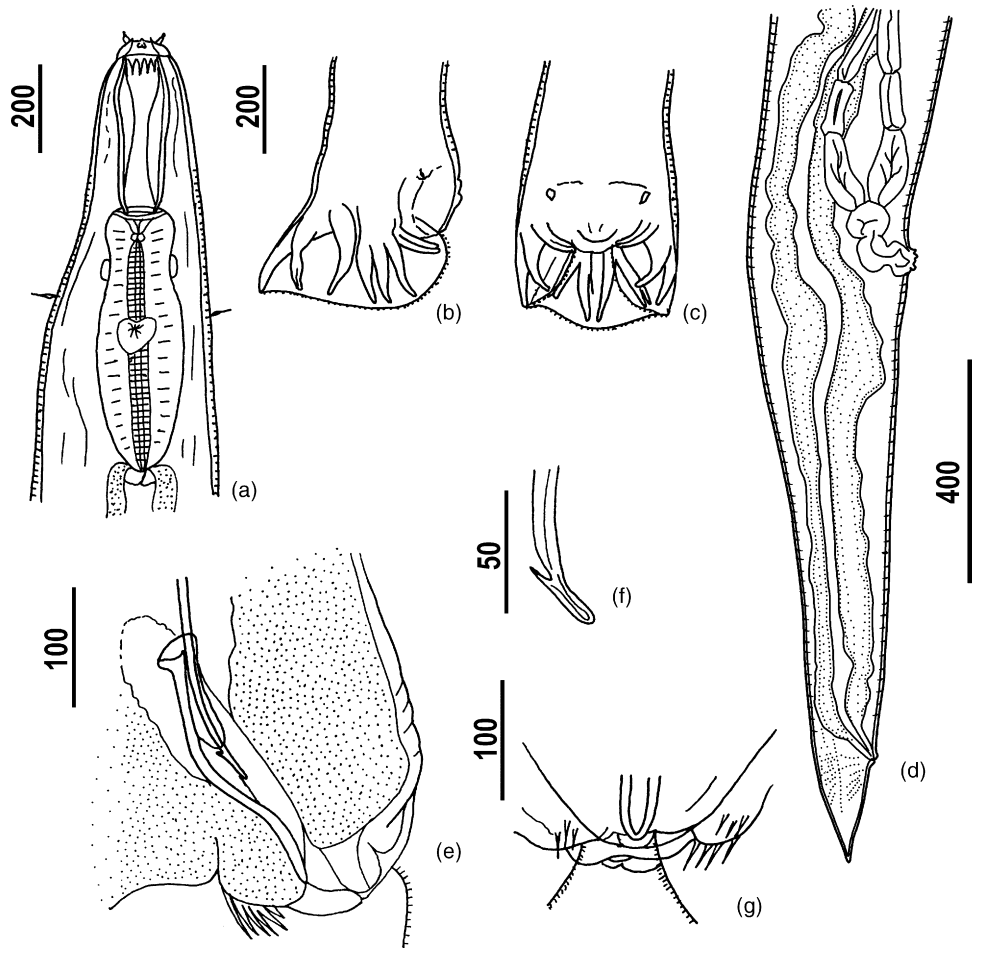

Fig. 119. *Cylindropharynx intermedia*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Fused spicule tips of male. (g) Tip of genital cone, ventral view.

end to: deirids 603–788; excretory pore 649–823; NR 440–522. Vulva to tail tip 1.14–1.86 mm. Anus to tail tip 224–336. Egg size 56–61 × 95–106.

Hosts. *E. burchelli*, *E. zebra hartmannae*.

Locality. Cecum, colon.

Distribution. Africa.

6.11.4. *C. longicauda* Leiper, 1911 (Figs. 121 and 122)

Synonyms. *C. asini* Roetti, 1947.

General. Buccal cavity oval.

Male. Body length 4.7–7.8 mm. Esophagus length 397–450. BC width 54–90, depth 180–230. Anterior end to: deirids 347–481; excretory pore 336–504; NR 308–352. Spicule length 710–890. Gubernaculum length 162–196. Dorsal ray length 196–336. Dermal collar well-developed on ventral side of genital cone. Appendages of genital cone as in type species. Protrusions of dermal collar absent.

Female. Body length 6.2–8.5 mm. Esophagus length 420–500. BC width 54–100, depth 160–246. Anterior end to: deirids 431–520; excretory pore 420–515; NR 347–392. Vulva to tail tip 1.10–1.58 mm. Anus to tail tip 263–336. Egg size 84–95 × 44–56.

Hosts. *E. asinus*, *E. caballus* × *E. asinus*, *E. burchelli*, *E. zebra hartmannae*.

Locality. Cecum, colon.

Distribution. Africa.

6.11.5. Discussion

Previously, eight species of the genus were described. Although they are common parasites of zebras, most species were described on the base of only a few specimens. Firstly, Leiper (1911) created the genus *Cylindropharynx* for two species from zebras in

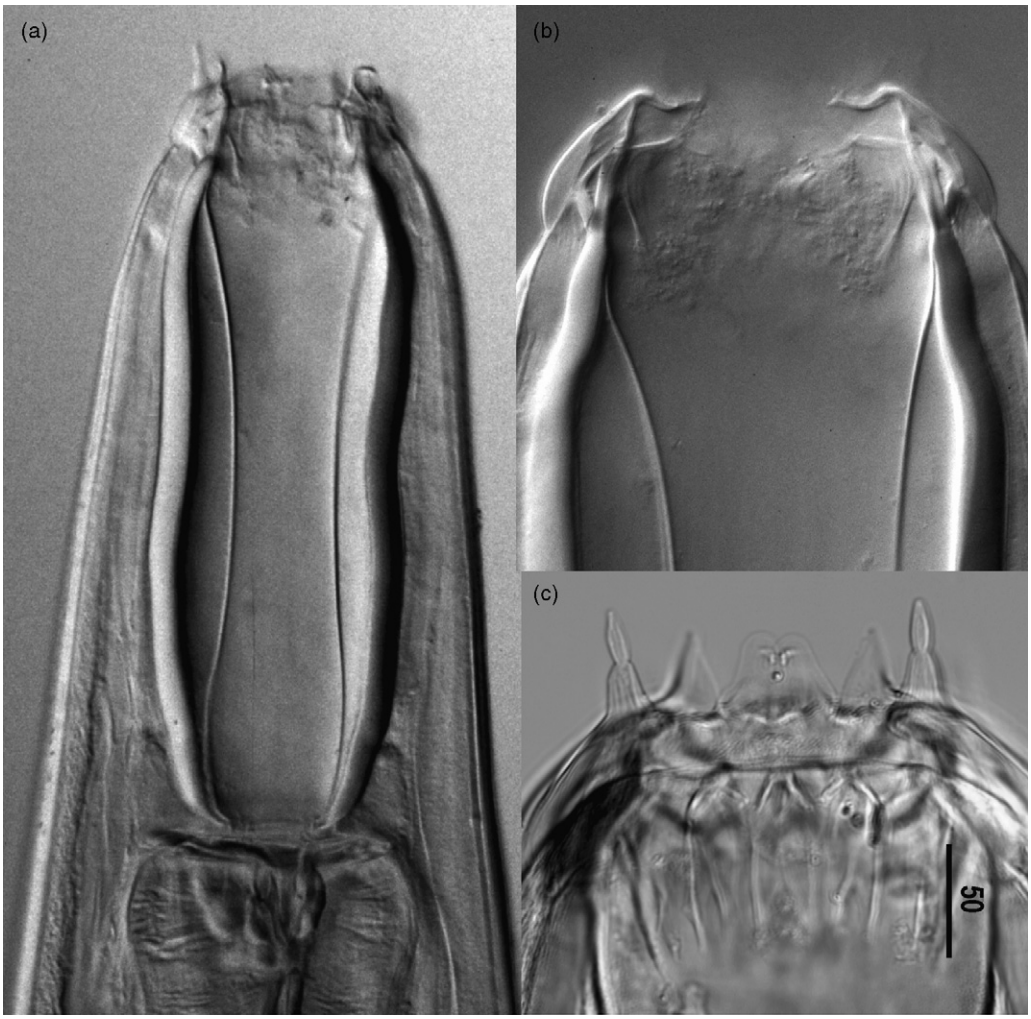

Fig. 120. *Cylindropharynx intermedia*. (a) Buccal capsule, dorsoventral view. (b) Anterior edge of buccal capsule, mouth collar and elements of ELC and ILC, lateral view. (c) Submedian papillae, elements of ILC and ELC, dorsoventral view.

British East Africa (now Kenya). Leiper's two species, *C. brevicauda* and *C. longicauda*, differed by size of buccal capsule, distance from vulva to tip of tail, spicule length and form of the external branch of the dorsal ray. Boulenger (1920) improved Leiper's description by describing the ELC and ILC and was first to pay attention to the structure of the genital cone appendages. He described peculiar appendages for *C. brevicauda*, that consisted of a pair of finger-shaped appendages with rounded ends just behind the genital opening, and an irregular number of delicate pointed processes scattered over the dorsal surface of the cone. According to Boulenger, *C. longicauda* has a single pair of rather stout finger-shaped processes.

Yorke and Macfie (1920) described *C. rhodesiensis*, a large species of the genus, with a vulva to tail tip distance of 1.7–2.2 mm. The authors had only one male and five females and were not able to distinguish appendages of the genital cone.

Theiler (1924) described *C. intermedia*, a species which differed from *C. brevicauda* by greater size and a vulva to tail tip distance of 1.5–1.6 mm. According to Theiler, *C. intermedia* differed from *C. rhodesiensis* by the nature of its genital cone. She noted that appendages of the genital cone in *C. intermedia* were the same as in *C. brevicauda*. Approximately at the same time, Cram (1925) described *C. ornata*. She also paid attention to structure of the ELC and appendages of the genital cone. Cram was not aware of Theiler's description of *C. intermedia*.

Two species, *C. aethiopica* and *C. asini*, were described from donkeys and mules in Ethiopia by Roetti

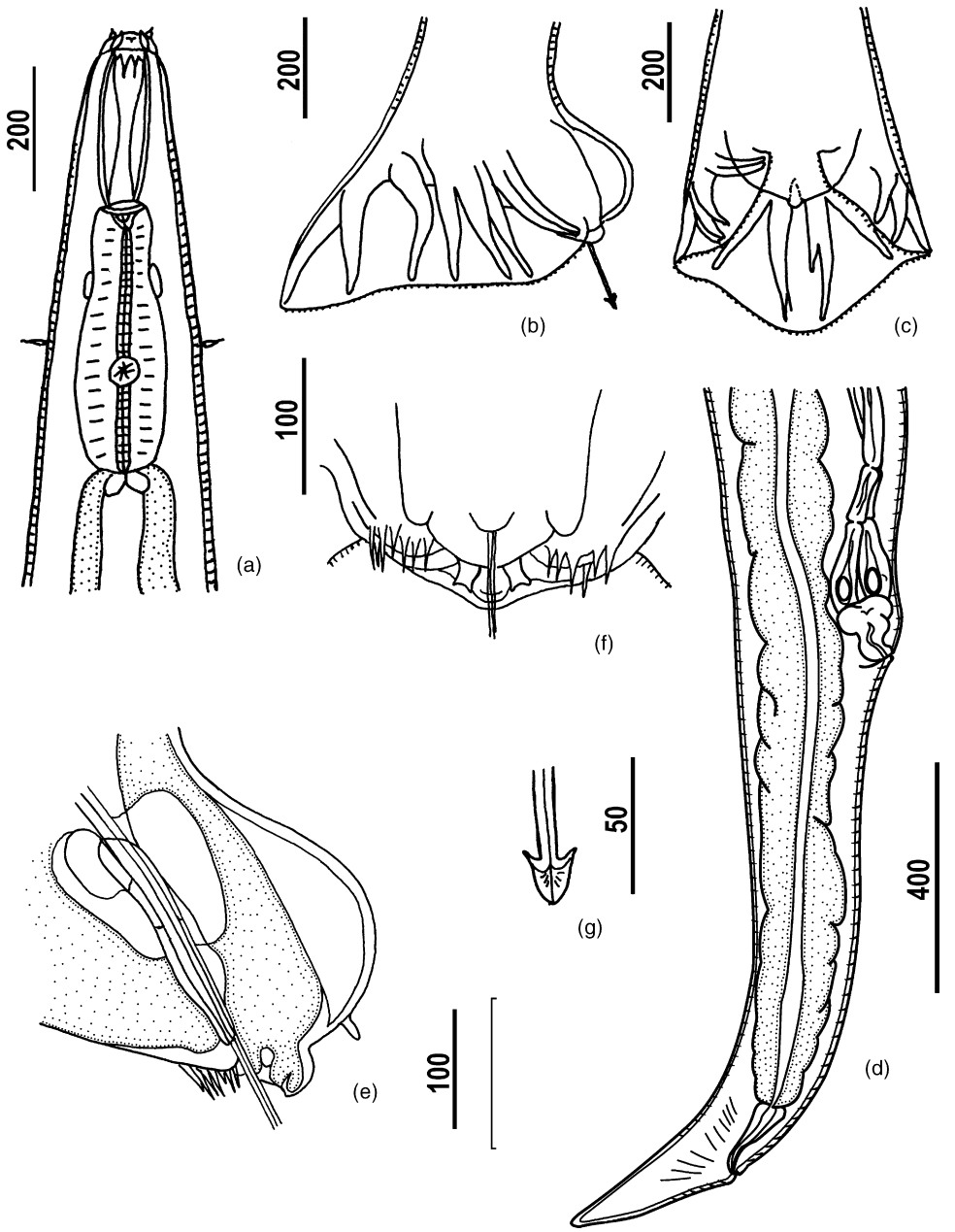

Fig. 121. *Cylindropharynx longicauda*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Genital cone, lateral view. (f) Tip of genital cone, ventral view. (g) Fused spicule tips of male.

(1947). He noted that his species differed from *C. brevicauda* and *C. longicauda* correspondingly only in measurements.

Lastly, *C. dollfusi* was described by Le Van Hoa (1962). This species was described with an oval genital cone, without appendages, rounded tips of dorsal ray and, according to the author, it was very similar to *C. rhodesiensis* from which it was distinguished by size.

We have studied all specimens of this genus which we were able to locate in museums around the world. That includes *C. dollfusi* from the Paris museum of natural history, *C. brevicauda* from Berlin Museum, *C. intermedia* from Onderstepoort Museum, *C. brevicauda*, *C. longicauda* and *C. intermedia* from British Museum and *C. ornata* from the U.S. National Parasite Collection. In addition, we have studied large numbers of specimens collected by

R. C. Krecek from zebras. We were not able to locate types of *C. asini*, *C. aethiopica* or *C. rhodesiensis.* Two of these species were never reported after their descriptions, and the last was mentioned twice in faunistic lists (Le Roux, 1932 and van den Berghe, 1943).

We treat *C. aethiopica and C. asini* as synonyms of *C. brevicauda* and *C. longicauda* correspondingly, because of insignificant differences in measurements of these species.

C. rhodesiensis is very similar to *C. intermedia*. However, we consider it as *species inquirenda* because it differs from other species by the extremely large size of the body and buccal capsule and a lack of appendages on the genital cone.

The type specimens of *C. ornata* are mounted on slides in balsam and it is impossible to study these specimens. Considering: that this species was described when the author did not have information about the similar species, *C. intermedia*; that based on the

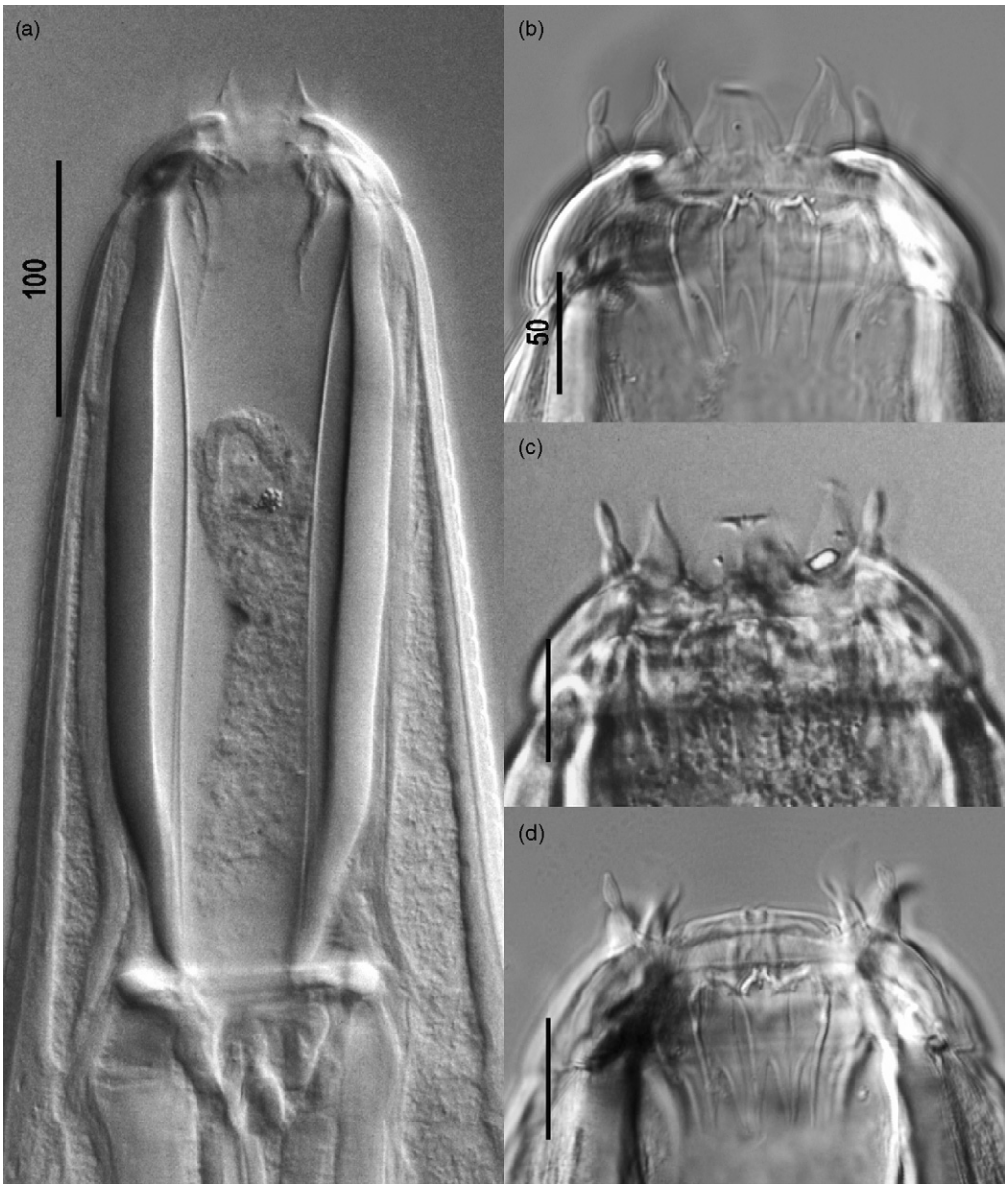

Fig. 122. *Cylindropharynx longicauda*. (a) Buccal capsule, dorsoventral view. (b) Elements of ELC and ILC and mouth collarlateral view. (c) Submedian papillae and elements of ELC. (d) Submedian papillae, elements of ELC and ILC lateral view.

drawing, the length of the buccal capsule is about 350 μm instead of 300 as listed in the text; and, that the appendages of the genital cone of *C. intermedia* can vary significantly, especially the pair of finger-shaped appendages (Scialdo-Krecek, 1984, our data); we treat *C. ornata* as a synonym of *C. intermedia*.

We also consider *C. dollfusi* to be a synonym of *C. intermedia* after studying the type specimens. We have found, that this species also has at least scattered irregular numbers of delicate pointed processes over the dorsal surface of the genital cone. We do not consider other peculiarities, such as thickness of dorsal ray branches or shape of their tips to be useful characters because of their variability within species of *Cylindropharynx*.

We also have found both kinds of genital cone appendages in *C. longicauda*.

6.12. *Caballonema* Abuladze, 1937

Synonyms. *Sinostrongylus* Hsiung and Chao, 1949.

General. Medium-sized Cyathostominea. MC flattened, undivided into inner and outer rings. Posterior edge of MC situated at anterior edge of BC. Amphids not markedly projected through MC surface. Submedian papillae extend through MC. Tip of submedian papillae long, uniform thickness, about three times as long as thick. Stalk of submedian papillae longer than broad. ELC markedly less numerous and longer than ILC. Elements of ELC as long as broad, tips pointed, triangular; insertion point on tips of ILC. Elements of ILC much broader than long, tips rounded; insertion on anterior edge of BC. Line formed by insertion of elements of ILC straight. Form of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with, and hood-like at anterior edge of BC; thick, bilayered, triangular in optical section. Septum intracoronare origin on support. Medial insertion of septum intracoronare situated at junction of ELC and ILC. Walls of BC concave, thicker in middle; thinner and curving medially anteriorly and posteriorly. Buccal cavity much deeper than wide, cylindrical. Dorsal gutter elongate, about $^{2}/_{3}$ depth of BC. Buccal teeth absent. Esophageal funnel moderately enlarged, rectangular, lined with thick cuticle. Esophageal teeth prominent. Anterior muscular portion of esophagus less than $^{1}/_{4}$ of esophagus length. Excretory pore near posterior end of esophagus. Deirids near middle of glandular esophagus.

Male. Dorsal ray with six branches; proximal branches much shorter than others. Ventral rays equal to laterals. Dorsal lobe much longer than laterals. Externodorsal rays origin at junction of dorsal and laterals. Gubernaculum thin, dorsal handle small to medium-sized and ventral notch prominent. Genital cone short, conical. Spicule tips pick-shaped.

Female. Vulva more than one tail length from anus. Vagina longer than sphincter of ovejector. Ovejector vestibule Y-shaped, infundibulum about equal to sphincter. Tail conical, long, more than 2× diameter at anus.

Type species. *C. longicapsulatum* Abuladze, 1937.

6.12.1. *C. longicapsulatum* Abuladze, 1937 (Figs. 123 and 124)

Synonyms. *Caballonema longispiculata* Kopyrin and Burikova, 1940; *Sinostrongylus longibursatus* Hsiung and Chao, 1949.

General. With characteristics of the genus. ELC consists of eight large, triangular elements. ILC consists of 16 short plate-like elements.

Male. Body length 6.3–12.5 mm. Esophagus length 460–490. BC width 126–187, depth 291–354. Anterior end to: deirids 660–720; excretory pore 655–747. Spicule length 1.42–2.25 mm, Gubernaculum length 224–266. Dorsal ray length 1.16–1.45 mm. Ventral rays length equal to laterals. Dermal collar well-developed on ventral side of genital cone. Genital cone appendages finger-like. Protrusions of dermal collar absent.

Female. Body length 12.0–16.0 mm. Esophagus length 520–624. BC width 142–189, depth 312–357. Anterior end to: deirids 675–748; excretory pore 680–776. Vulva to tail tip 1.07–1.26 mm.Anus to tail tip 478–520. Egg size 98–112 × 47–54.

Hosts. *Equus caballus*.

Locality. Cecum, colon.

Distribution. Asia.

6.12.2. *Discussion*

This genus was grouped with *Cylindropharynx* in the Tribe Cylindropharyngea by Popova (1958), but we prefer to emphasize the similarities among the Cyathostominae of horses and, following Lichtenfels (1980), consider them to belong to a single tribe, the Cyathostominea. A phylogeny to test this hypothesis is needed.

6.12.3. *Gyalocephalus* Looss, 1900

General. Medium-sized Cyathostominae. MC high, divided into inner and outer rings. Posterior edge of MC posterior to edge of BC. Amphids not markedly projected through MC surface. Submedian papillae extend through MC. Tip of submedian papillae cone-

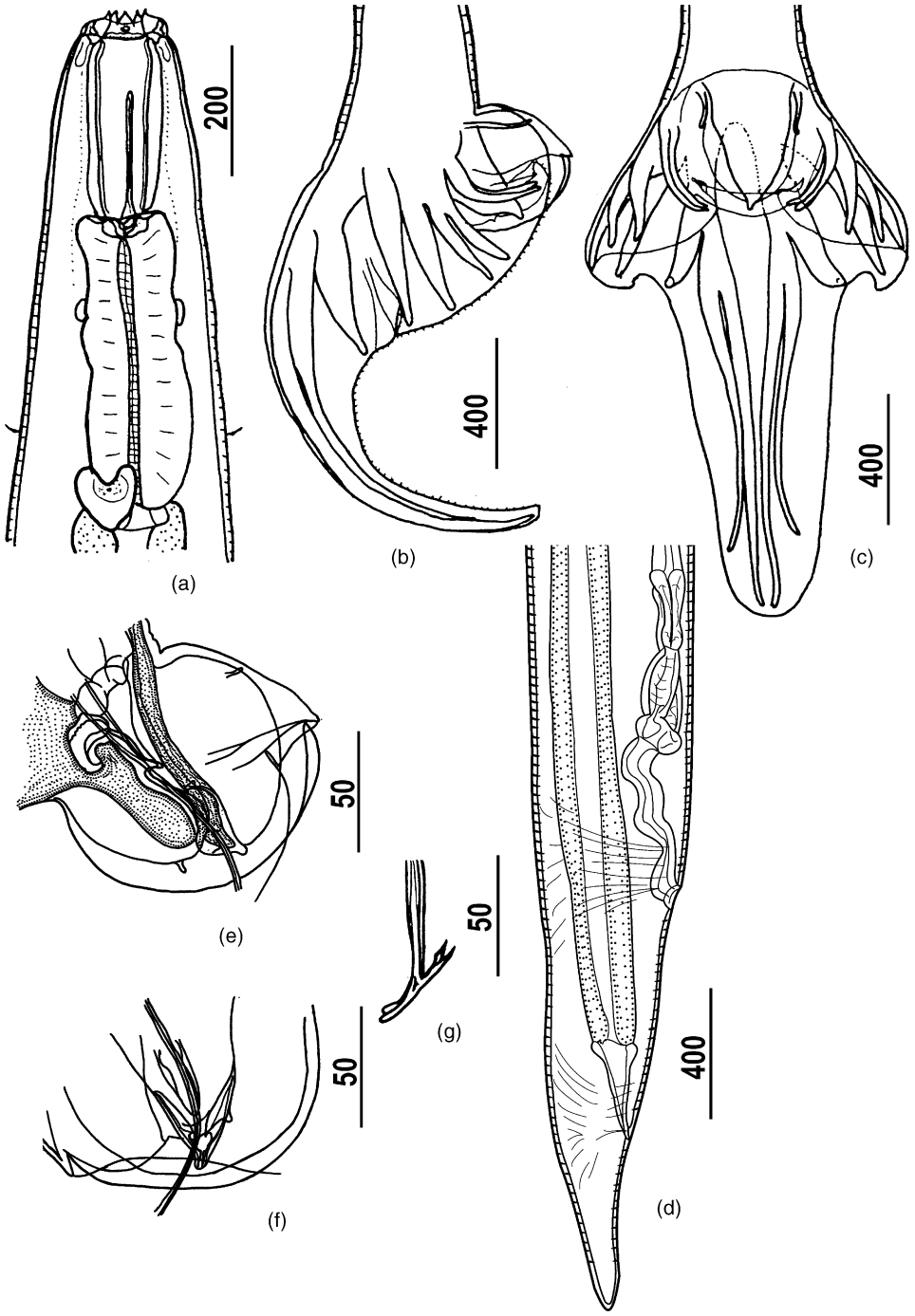

Fig. 123. *Caballonema longicapsulatum*. (a) Esophageal region, ventral view. (b) Male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female, lateral view. (e) Male genital cone, lateral view. (f) Tip of male genital cone, ventral view. (g) Fused spicule tips (modified from Dvojnos and Kharchenko, 1994).

shaped one to two times as long as thick. Stalk of submedian papillae longer than broad. Elements of ELC markedly more numerous and shorter than elements of ILC. Elements of ELC longer than broad, tips pointed; insertion point on tips of ILC. Elements of ILC longer than broad, tips pointed; insertion on medial shelf of BC more than $^1/_2$ of BC depth. Line formed by insertion of elements of ILC straight. Form

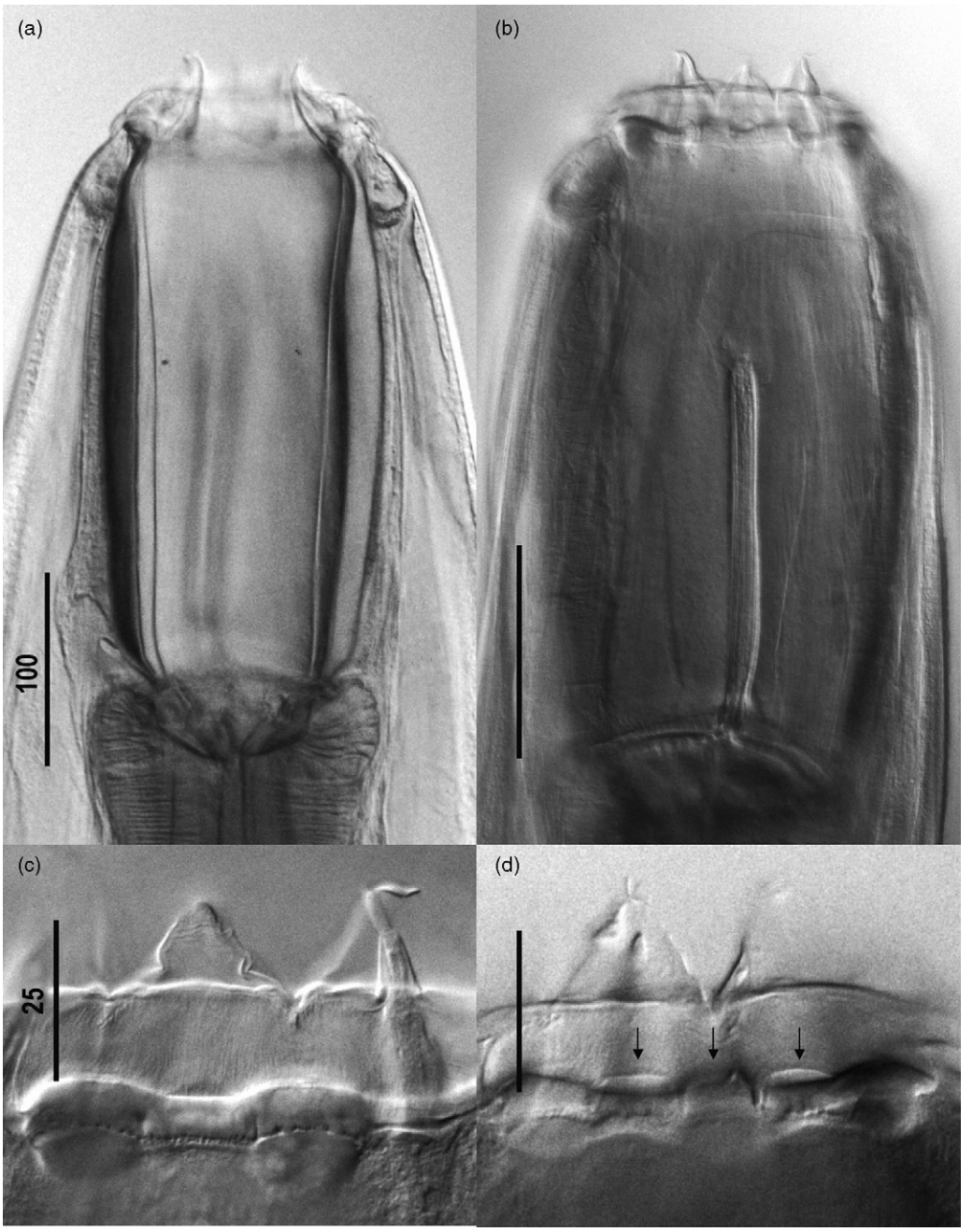

Fig. 124. *Caballonema longicapsulatum*. (a) Buccal capsule, dorsoventral view. (b) Anterior end, dorsal view showing long, thin dorsal gutter. (c) Anterior end, dorsal view, showing submedian papilla, large triangular tips of elements of ELC and bilayered support for ELC that hoods anterior edge of BC. (d) Anterior end, dorsal view, showing short, broad plate-like elements of ILC (arrows) medial to support.

of posterior edge of elements of ILC straight, unadorned. Support for ELC continuous with BC, short, triangular in optical section. Septum intracoronare origin on BC. Medial insertion of septum intracoronare situated anterior to junction of ELC and ILC. Walls of BC broadest anteriorly, much narrower posteriorly; with medial, arch-like posterior projections that support each element of the ILC. Buccal cavity wider than deep, wider posteriorly. Dorsal gutter inconspicuous. Buccal teeth absent. Esophageal funnel greatly enlarged; cuticular lining modified to form, in each of three esophageal sectors, bifid sickle-shaped projections. Esophageal teeth at base of esophageal funnel. Anterior muscular portion of

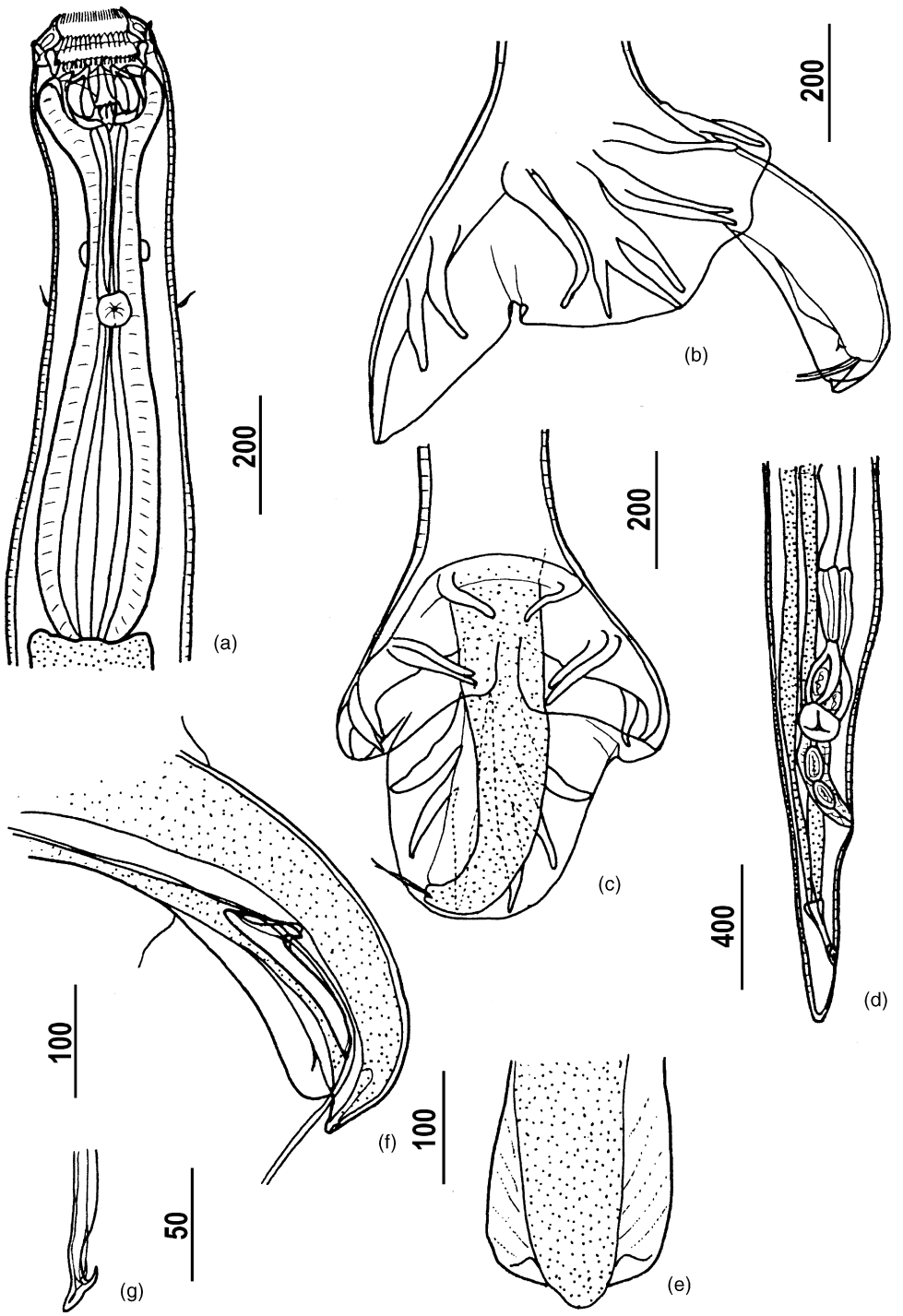

Fig. 125. *Gyalocephalus capitatus*. (a) Esophageal region, ventral view. (b) male tail, lateral view. (c) Male tail, dorsoventral view. (d) Tail of female. (e) Tip of genital cone, ventral view. (f) Genital cone, lateral view. (g) Fused spicule tips of male (modified from Dvojnos and Kharchenko, 1994).

esophagus about 1/4−1/3 of esophagus length. Excretory pore posterior to NR. Deirids at level of NR.

Male. Dorsal ray with six branches. Ventral rays longer than laterals. Dorsal lobe longer than laterals. Externodorsal rays origin at junction of dorsal and laterals. Gubernaculum large, without dorsal handle, but with ventral notch. Genital cone elongate, extends beyond bursal edge. Spicule tips hook- or harpoon-shaped.

Female. Vulva more than one tail length from anus. Vagina longer than sphincter of ovejector. Ovejector vestibule oval or Y-shaped, infundibulum longer than sphincter. Tail conical, short, less than 2× diameter at anus.

Type species. *G. capitatus* Looss, 1900.

6.12.4. *G. capitatus* Looss, 1900 (Figs. 125–127)

Synonyms. *Gyalocephalus equi* Yorke and Macfie, 1918.

General. With characteristics of the genus. Elements of ELC markedly shorter and more numerous (90–95) than ILC (30–34).

Male. Body length 7.0–9.5 mm. Esophagus length 852–970. BC width 150–158, depth 59–64. Deirids to head end 405–409. Spicule length 1.18–1.2 mm. Gubernaculum length 160–177. Dorsal ray length 580–650. Ventral rays longer than laterals. Dermal collar poorly developed on ventral side of genital cone.

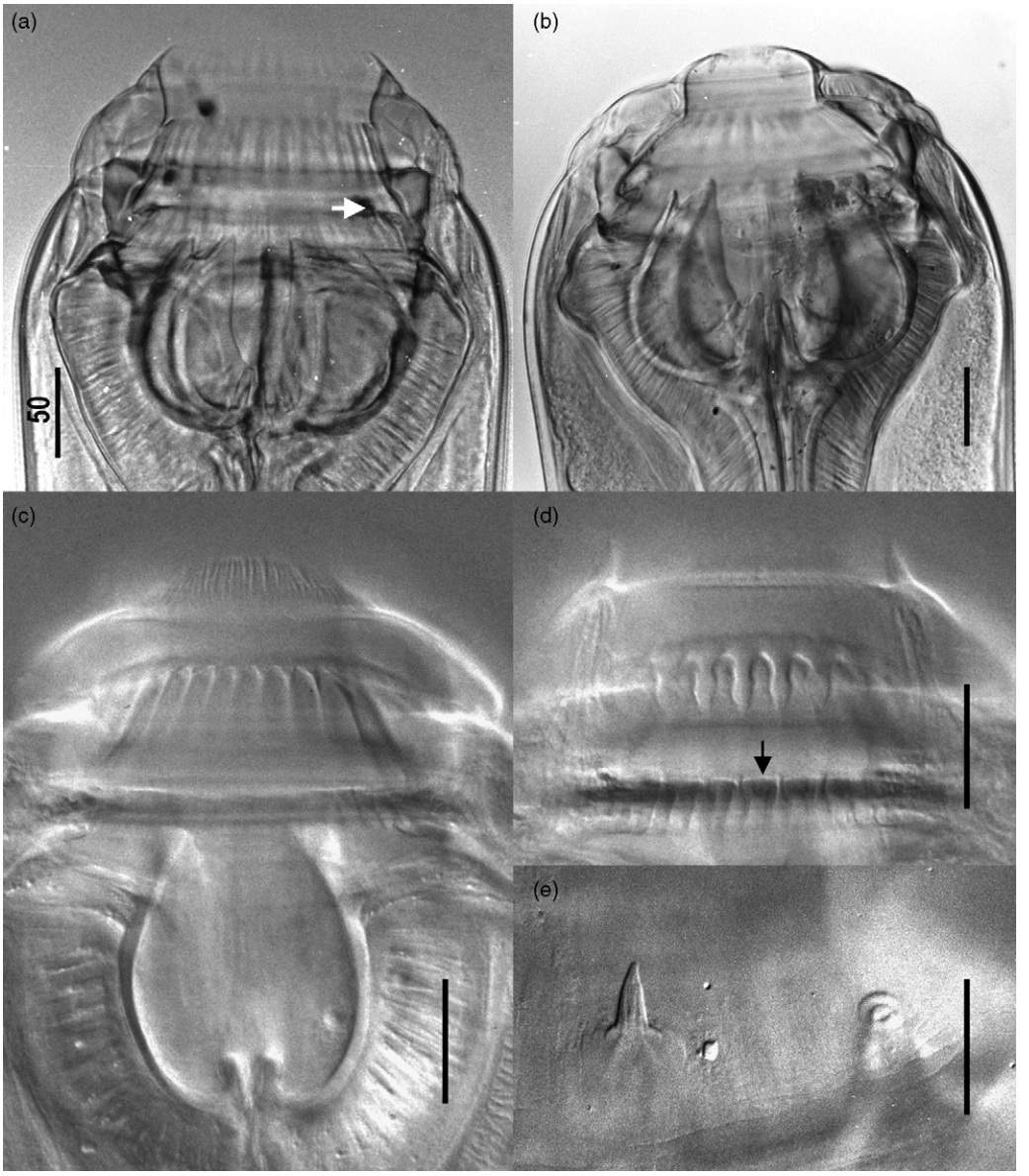

Fig. 126. *Gyalocephalus capitatus*. (a) Buccal capsule, dorsoventral view, showing ELC, ILC and esophageal funnel. Arrow marks medial shelf-like projection of buccal capsule that supports elements of ILC. (b) Buccal capsule, lateral view. (c) Buccal capsule, subventral view, showing elements of ELC and ILC. (d) Dorsal view of 2 submedian papillae, elements of ILC and medial shelf-like projection of BC (arrow) that supports elements of ILC. (e) Sublateral view of mouth collar showing subventral papilla (on left) and lateral papilla (on right).

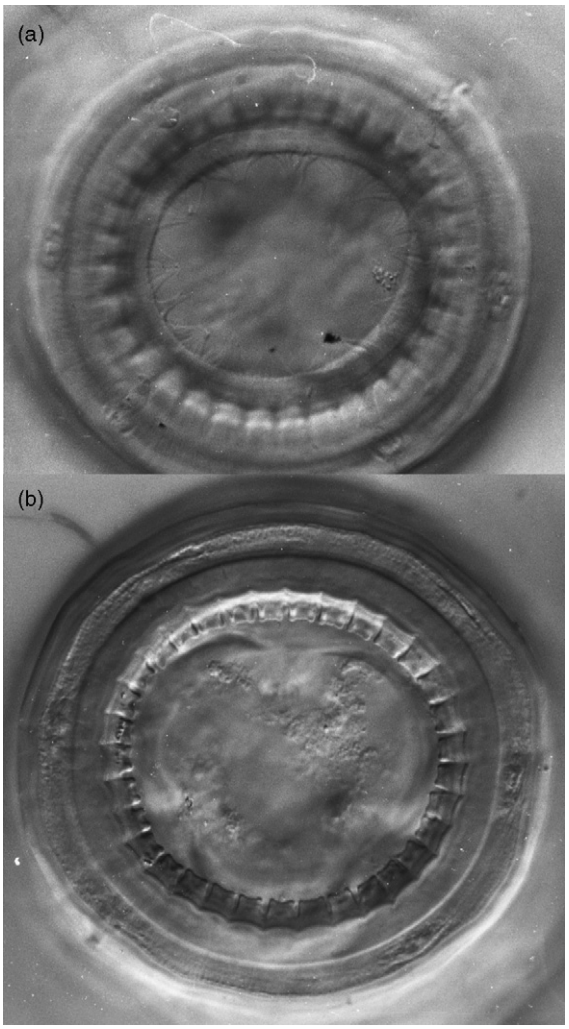

Fig. 127. *Gyalocephalus capitatus*, en face. (a) Optical section at level of ILC. (b) Optical section at level of projections at base of BC.

Appendages of genital cone paired, finger-like. Protrusions of dermal collar absent.

Female. Body length 10.5–11.0 mm. Esophagus 1.20–1.38 mm. BC width 170–174, depth 64–68. Vulva to tail tip 593–657. Anus to tail tip 211–296. Egg size 90–118 × 50–68.

Hosts. *Equus caballus*, *E. asinus*, *E. caballus* × *E. asinus*, *E. przewalskii*, *E. hemionus*, *E. burchelli*.

Locality. Cecum, colon.

Distribution. Cosmopolitan.

6.12.5. Discussion

Hartwich (1986) retained *Gyalocephalus*, following Popova (In Skrjabin et al., 1952), in the tribe Gyalocephalea based on its distinctive head characters, enlarged esophageal funnel, and intestinal organization, which they considered to represent differences from other Cyathostominae at greater than generic level. We prefer to emphasize similarities among members of the subfamily, following Lichtenfels (1980), and include *Gyalocephalus* in the Cyathostominea.

7. Phylogeny

Previously published phylogenetic studies of the Strongyloidea of horses have all been based on molecular characters (Hung et al., 2000; McDonnell et al., 2000). An unpublished morphological phylogeny of 23 genera of Strongyloidea of horses (Lichtenfels and Hoberg, unpublished, presented at 1999 Workshop, "Systematics of the Cyathostominea of Horses", World Association for the Advancement of Veterinary Parasitology, Copenhagen, 1999; see Lichtenfels et al., 2002) provided information that concurred with some conclusions of the molecular studies, but differed in others. Both molecular and morphological phylogenies grouped the genera *Oesophagodontus*, *Craterostomum*, *Triodontophorus* and *Bidentostomum* (previously included in the Strongylinae with Strongylus) with the Cyathostominae. Numerous previous workers have speculated (see Lichtenfels, 1979; Gasser et al., 2004) that the subfamily classification of the Strongyloidea may not represent natural groups. However, we believe a revision of the subfamily classification should await the publication of a more complete generic morphological phylogeny. Both molecular and morphological phylogenies identified a common clade of genera of Cyathostominea, including the genera *Cyathostomum*, *Coronocyclus*, *Cylicocyclus*, *Cylicostephanus*, *Petrovinema*, and *Tridentoinfundibulum*. The major difference between the molecular and morphological phylogenies was the failure of the former to resolve the genera within the above common clade, but all were resolved by the latter. A morphological phylogeny of the Cyathostominea has not been published and it is considered beyond the scope of this treatise. We hope the results presented here will stimulate additional phylogenetic studies of these species. For the present, the morphological characters are sufficient to identify the species. The taxonomy employed is consistent with our current knowledge of the phylogenetic relationships within these economically important nematode parasites of horses. The development of molecular methods to identify species should be recognized as a critical need. We believe the studies presented here will be essential to meet these and other research needs related to these nematodes.

8. Alphabetic index of genera, subgenera, species, and subspecies including synonyms

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